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THE QUARTERLY REVIEW OF BIOLOGY

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THE QUARTERLY REVIEW of BIOLOGY



THE AGASSIZ-ROGERS DEBATE ON EVOLUTION

By W. M. SMALLWOOD

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THERE have been three notable debates on the general subject of what we now term "evolution." The first was between Georges Léopold Chrétien Frédéric Cuvier (1769-1832) and Geoffroy Saint-Hilaire (1772-1844). We shall refer but briefly to this controversy which stirred intellectual Europe.

The well-known Huxley-Wilberforce debate at Oxford was the third and most widely-publicized of the three. It was the least important as an analysis of the real problems involved, but probably carried more weight with the English-speaking world than either of the other two.

Chronologically, the Agassiz-Rogers debate began six months before the British Association met at Oxford. The following brief notes on the first and third debates afford a basis for comparison and the literature necessary for a more comprehensive analysis.

THE CUVIER-SAINT-HILAIRE DEBATE

It was on February twenty-second, 1830, that these two intellectual giants began

their controversy in Paris before the members of the Académie de Sciences. Both were high-spirited, impulsive men, and leaders in the expanding field of comparative anatomy. Cuvier had formulated his catastrophic theory and his correlation theory. Saint-Hilaire was inclined to philosophize on the existence of a common basis of organization of all vertebrates, a philosophy which he extended to include the entire animal kingdom. This led him to make fantastic comparisons; and the following citation reveals how far his explanation departed from our modern ideas of genetic continuity: "In a word, we see here, whatever Bonnet and his followers may have said, nature pass from one plan to another, make a jump, leave between her productions a manifest gap. The mollusks are not intermediary to anything; they are the result of the development of other animals, and their own development has produced nothing superior to them" (1).

Cuvier and Saint-Hilaire had been friends and co-workers for a long time; but the speculations of the latter brought

them to open argument when Geoffroy Saint-Hilaire read a paper on the "Organization of the Cephalopods," written by two young naturalists, Latreille and Meyranx. By this act, he gave his endorsement to their endeavor to show that the organization of cephalopod mollusks could be "assimilated," as they expressed it, to the vertebrates. We now consider the change they proposed as absurd: "They imagined a vertebrate to be bent double at the height of the navel, so that the ventral surface should remain outside and the two halves of the back, brought into contact, should be joined together" (2). This comparison between the squid (ink-fish) and a fish was more than Cuvier could endure in silence.

There is no complete record of exactly what was said in the several encounters between these two debaters. In Saint-Hilaire's mind, back of the comparisons of structures which were made, existed what he called *d'unite de plan*. This struck at the very basis of Cuvier's own classification of animals into four groups. "But what," Cuvier asked, "is *unity of plan*, and especially *unity of composition*, which is to serve henceforth as a new basis for zoology? These words evidently cannot be employed in the ordinary sense, in the sense of *identity*; for a polyp and even a whale, or an adder, do not possess all the organs of a man, placed in a similar way; the words *unity of plan*, *unity of composition* signify then simply, in the mouth of those who use them, *resemblance*, *analogy*" (3).

Saint-Hilaire then substituted *methodé des analogues*, and maintained that his explanation was entirely *new* and that Cuvier was holding that *structure* had been the basis of distinction since Aristotle's time. The method of analogies is independent of unity of plan, and has been used down to the present day. These

discussions before the Académie lasted for a year, then were continued for two years longer in public lectures at the Collège de France (4).

This debate destroyed a friendship of long standing. Cuvier won before the Académie, but the man on the street was with Saint-Hilaire. The arguments presented by Saint-Hilaire comprised six problems that are not yet solved in their entirety: (1) the pre-existence in natural history of the genus; (2) the unity of organic composition; (3) the value of classification; (4) the fixity of species; (5) the final cause; and (6) the succession of organic life on earth (5).

These arguments, carried on over a period of three years, proceeded from the complex to the simple. Saint-Hilaire attempted to transform a fish into a squid. Man was the center of the philosophical universe; and the present-day historical or genetic method of thinking does not appear until we come to the Huxley-Wilberforce-Hooker and the Agassiz-Rogers debates.

THE HUXLEY-WILBERFORCE-HOOKER DEBATE

The summer meeting of the British Association was held at Oxford in 1860, and the first three days were devoted to the reading of papers. It had been rumored that the *Origin of Species* would come up for criticism. Hooker, the confidant of Darwin, did not attend the Thursday sessions, but wandered about the familiar streets. It was from his letter to Darwin that we learn of the beginning of the sharp differences of opinions, climaxing on Saturday in the debate in which he, Huxley, and the Bishop of Oxford participated.

During the informal discussion of Dr. Daubeny's paper, "On the final causes of sexuality in plants, with particular reference to Mr. Darwin's work on the Origin

of Species," the chairman called on Huxley who was reluctant to consider the general question of the truth of Darwin's theory. "He felt that a general audience, in which sentiment would unduly interfere with intellect, was not the public before which such a discussion should be carried on," (6) and that Dr. Daubeny had, in fact, brought forth nothing new.

Professor Owen then proceeded to give his personal opinions of similarities and differences between man and the monkey. Taking the brain of the gorilla, "it presented more differences, as compared with the brain of man than it did when compared with the brains of the very lowest and most problematical form of the Quadrumana. The deficiencies in cerebral structure between the gorilla and man were immense" (7).

The official report refers only briefly to Huxley's reply to Owen; but in one story of the meeting he is said to have retorted in this challenging manner: "I must directly and unequivocally contradict the statement. My procedure is unusual, but seems necessary. I shall justify it elsewhere" (8). This he did in his book, *Man's Place in Nature*, also in the *Natural History Review*.

The meetings on Friday were taken up with the reading of papers which held but passing interest. It was not until the Saturday program that a large audience was attracted to this sectional meeting of Zoology and Botany to listen to a contribution by Professor Draper of New York, "On the Intellectual Development of Europe, considered with Reference to the Views of Mr. Darwin and others, that the Progression of Organisms is determined by law" (9).

The room in which this section first assembled was so small that it was found necessary to adjourn to the Library of the New Museum; and that also became

crowded to suffocation. There were several participants in the discussion of Dr. Draper's paper before the Bishop of Oxford began his address. It is very interesting to contrast the official report of the meeting with the personal accounts of some of the eye-witnesses. The mere fact that both Hooker and Huxley were urged to be present indicates that the opponents of Darwin had made extensive plans to "smash Darwin" (10), for which purpose they had selected "Soapy Sam" (11) Wilberforce, as the Bishop of Oxford had been known when an under-graduate. Samuel Wilberforce spoke for half an hour, and had evidently been coached by Owen. He received great applause from his adherents who occupied the center of the auditorium. At the close of his address, he made reference to Huxley's genealogy in words which apparently no one took the trouble to record accurately, although the question implied that one of Huxley's grandparents must have been related to an ape. There are two or more versions of the phrasing of Bishop Wilberforce's question, and we find the same confusion in regard to Huxley's reply:

I asserted, and I repeat, that a man has no reason to be ashamed of having an ape for his grandfather. If there were an ancestor whom I should feel shame in recalling, it would be a *man*, a man of restless and versatile intellect, who, not content with an equivocal success in his own sphere of activity, plunges into scientific questions with which he has no real acquaintance, only to obscure them by an aimless rhetoric, and distract the attention of his hearers from the real point at issue by eloquent digressions, and skilled appeals to religious prejudice (12).

Huxley was followed by Hooker, the botanical friend of Darwin, who had been confidentially told about natural selection as far back as 1844—a fact which gave him a decided advantage in the argument. Hooker had been very reluctant to enter the controversy until the Bishop's address had revealed his unfairness, as we

learn from this unpublished letter to Asa Gray:

I spoke only once, the last of all; showed that he [the Bishop] could never have read Darwin's book and exposed ignorance of the rudiments of science—I shut him up completely, *he had not a word to reply*, and the discussion was closed amid rounds of applause for my side (13).

When we compare this debate with that between Cuvier and Saint-Hilaire, we realize that it was not so much a discussion between two eminent scientists as a struggle between science on the one hand, and the church on the other. Huxley gained great notoriety for his retort, while the Bishop's statements have brought him lasting ridicule. Though the understanding and importance of natural selection was not appreciably advanced by the manner in which this highly-emotional controversy was conducted, it is the most widely-quoted of all debates over Darwin's theory. The good sportmanship of the English gave a hearing to Huxley and Hooker, and the resulting publicity served to popularize evolution.

THE AGASSIZ-ROGERS DEBATE

Some may object to designating the successive discussions at the regular meetings of the Boston Society of Natural History (February 15, March 7, March 21, and April 4, 1860) as a debate. Though not announced as such in advance, the zeal with which it was carried on for months seems to justify this interpretation. The antagonists were that widely-known scientist, Louis Agassiz, and William Barton Rogers, later to become President of the Massachusetts Institute of Technology. Agassiz's popularity as a lecturer was conceded, and his winsome personality aided in the acceptance of his leadership. Rogers had left an enviable reputation in Charlottesville, Vir-

ginia, where he was highly regarded by the students during his eighteen years as professor of natural philosophy.

The personal charm and scientific attainments of Louis Agassiz are well known. If we are to enjoy this famous contest, it is desirable to outline some of Rogers's qualities and achievements. Professor Rogers had been doing pioneer research in geology for thirty-two years and, with his brother Henry, had initiated geological surveys in Virginia, Pennsylvania, and New Jersey. The history of American geology places their names in the front rank:

By 1844, the Rogers brothers had planned their nomenclature and classification of the Appalachian Paleozoic and later formations. They recognized that, in some places, Paleozoic rocks exceed 30,000 feet in thickness, are made up of a variety of sediments, and represent a profound lapse of time. Their subdivisions of the Paleozoic and later formations were made on the fossil content, mineral character, and relative expansion of the formations. This scheme was followed for many years, and, as late as 1900, it had not been completely abandoned (14).

When the English edition of the *Origin of Species* was first published, Henry Rogers was in Scotland. The following brief extracts from the letters exchanged between William and his brother, Henry, give an intimate picture of the attitude of these two Scottish-Americans toward natural selection, even before the American edition of the *Origin* was brought out by Appleton, in January, 1860.

Henry Rogers, writing to his brother from Glasgow, on December 23, 1859, expressed his opinion of the *Origin* in these words:

The only matter of any interest is the appearance of Charles Darwin's book, *On the Origin of Species by Means of Natural Selection*. It is a suggestive book, full of ingenious arguments in favour of the Lamarckian hypothesis. Huxley, who bitterly criticised the 'Vestiges,' has reviewed this work in terms of high commendation. When you read it you will

often say, I think, that in his geology Darwin outdoes Lyell himself in ignoring paroxysmal actions. This is its chief blemish with me.

On January 2, 1860, William replied from Boston:

I have been reading the early chapters of Darwin's book with great interest. . . . The more I look into Darwin's argument the more I like it, save in the one particular of ignoring entirely violent and sudden physical changes. The calmness and truth-loving spirit of the book are truly admirable. Much of it I know *you* will approve.

Later in that same month William again wrote:

The next number of 'Silliman' will contain an elaborate review of Darwin's book by Gray, who called some days ago to leave his proof sheets with me. He has not affixed his name, and requested me to say nothing of it for the present. I hear that Mr. Ticknor has just heard from Lyell, who speaks approvingly of Darwin's views. I anticipate many disciples for Darwin on this side of the Atlantic, in spite of the '*diastrous*' tendency of his views.

Lyell, I hear, is preparing another edition of his 'Elements,' and I presume he will introduce this subject, and the late evidences of the antiquity of man, as well as other new matter into it. . . .

How I long, my dear brother, to talk with you about these scientific matters. I have never felt so much the want of such communion.

When Henry replied to his brother's letter on February 24, 1860, he said:

I wrote to Huxley awhile since in relation to Darwin's book (15) and your liberal defence of it, and he replies much pleased. In a few years, opinion among the reflecting in Europe will be with Darwin, you may depend on it, as to the law of a natural selection. As to the other point, development of species from species, firmly as I believe in it, I think it will never be capable of a strictly scientific proof, no more can the opposite doctrine of supernatural creations, and therefore the main point to insist on now is toleration and no dogmatizing (16).

Thomas Henry Huxley, writing to Henry Rogers from London, on January 9, 1860, asked "Have you read Darwin?" He prophesied: "There will be great

fighting about his views for the next ten years, and great things will arise out of the combat." In another letter, written on the seventeenth of the same month, he told Rogers: "'Darwin' is the great subject just at present and everybody is talking about it" (17).

The historians of this period agree in describing both Agassiz and Rogers as unusually brilliant men as well as in their statements that the man who finally triumphed did not permit his emotions to betray him.

Let us now turn to this least-known but ablest of the three great debates over evolution.

The First Meeting, February 15, 1860

When the Boston Society of Natural History was called to order on February 15, 1860, Dr. C. T. Jackson, the Vice-President, was in the chair. The American edition of the *Origin of Species* had been off the press scarcely three weeks; but it is certain, from the letters of Rogers, that copies of the English edition had been available for some time.

Louis Agassiz opened the meeting with an attack on Darwin's "ingenious but fanciful theory." He supported his objections against variation by calling attention to the exceedingly long existence of the brachiopod, *Lingula*, which had not undergone any variations in practically its entire geological life span. Thus, with scientific data that seemed conclusive, the debate began. The record of this exchange of arguments is told in the language of the secretary, and not exactly as phrased by the contestants. The minutes of that first meeting report Agassiz as beginning in this fashion:

Mr. Darwin he acknowledged to be one of the best naturalists of England, a laborious and successful writer; his works on the coral reefs, on the cirripeds, and his narrative of the voyage of the *Beagle*, show

him to be a skilful and well prepared naturalist; but this great knowledge and experience had, in the present instance, been brought to the support, in his opinion, of an ingenious but fanciful theory. According to Darwin, the primary cell, by a process of differentiation and gradual improvement by natural selection, has produced all the diversities of animals, in geological and present times. He did not think it fair to compare the present fauna of the world with the fauna of any geological horizon as known in one locality; and he thought this method of comparison had led to this idea of gradual development (18).

Rogers replied to Professor Agassiz's objection over animals that persist for a long period without change, and

admitted that the persistency of *lingula*, and other similar cases that might be adduced, were formidable objections to this theory; but he thought that Darwin would meet such objections by the fact that the vital characters of some animals fit them for resisting change and extinction better than more plastic natures; from our knowledge of domesticated animals we find that dogs have changed very much, and that cats have changed hardly at all; some have great energy of resistance, and some very little (19).

The argument presented by Agassiz continued to be a stumbling-block for a long time; for we note that when Huxley, who had been expounding Darwinian evolution for seventeen years, visited the United States, he devoted considerable time to "persistent types" in his lecture on evolution. "It is obvious," said Huxley, "that, if it can be proved that animals have endured, without undergoing any demonstrable change of structure, for so long a period as four thousand years, no form of the hypothesis of evolution which assumes that animals undergo a constant and necessary progressive change can be tenable; unless, indeed, it be further assumed that four thousand years is too short a time for the production of a change sufficiently great to be detected" (20).

Huxley then listed the several fossil species known to have been in existence

for hundreds of thousands of years, and continued:

Facts of this kind are undoubtedly fatal to any form of the doctrine of evolution which postulates the supposition that there is an intrinsic necessity, on the part of animal forms which have once come into existence, to undergo continual modification; and they are as distinctly opposed to any view which involves the belief, that such modification as may occur, must take place, at the same rate, in all the different types of animal or vegetable life. The facts, as I have placed them before you, obviously directly contradict any form of the hypothesis of evolution which stands in need of these two postulates (21).

This was really a problem in variation; one that was not fully analyzed until the discussions on Mendelism and mutation. But, to return to the debate; Rogers next raised the question of migrations and possible re-migrations of extinct animals, a problem brought to the foreground when biogenesis became the accepted law of life and older explanations were no longer satisfactory. Rogers took a bold step, striking at one of Agassiz's most cherished views, when he applied this idea to his theories of animals that lived in the ancient world.

On the coast of Virginia and Maryland there is an extensive oyster-bed, but which has not been continuous through all time; at one time the oysters disappear, and clams make their appearance; the latter disappear, and oysters reappear; these he regarded as instances of emigration and remigrations over great spaces.

To this statement Professor Agassiz replied that: "As to these alleged migrations, we know that species are well circumscribed within the limits of faunæ; and . . . before such a line of argument can be followed, it must be shown that any species pass from one continent to another, except from man's agency" (22).

Rogers "inquired of Prof. Agassiz if any vertebrate had ever been found in strata lower than the upper Silurian"

(23); and Agassiz's reply summarized the widely-held belief regarding ancient forms of plants and animals. There was no basis for compromise in his assertion that "in this lowest system of fossils there was such a coordination of the animal series as shows that all its great and principal classes were then existing" (24).

The scientific argument was temporarily interrupted as the qualifications of Darwin were questioned by one of Agassiz's old friends, Emerson, who had failed entirely to understand Darwin's method:

Darwin comes before the reader at once as an advocate of a seemingly foregone conclusion, and argues, not for the purpose of finding in what direction the evidence of any particular fact would lead the mind, but for the purpose of finding something in the fact favorable to his preconceived opinion. Admitting the difficulties in his theory, he tries to explain them away by various suppositions and *ifs*, which by frequent repetition and consideration seem in the mind of the author to become established truths, and are used as arguments (25).

In correcting Mr. Emerson, Professor Rogers stated that:

... the present work of Darwin is a *résumé* of his conviction on the subject, without the presentation of the facts upon which it rests, which he has not had time to arrange. The problem is admitted to be of transcendent difficulty, and such as no observer or theorist can hope now or perhaps ever positively to resolve. Mr. Darwin makes no pretensions to an absolute demonstration, but, after an impartial survey of the facts bearing on the subject and a candid appreciation of the opposing considerations, adopts the view set forth in his book, as offering, in his opinion, a more rational and satisfactory explanation of the history of living nature than the hypothesis of innumerable successive creations. Prof. Rogers regarded the work as marked in an extraordinary degree by fairness in the statement of opposing as well as favorable arguments, by the absence of dogmatism, and by all other evidence of a truth-loving spirit, as well as by the extent and variety of its knowledge and the breadth of its philosophical views (26).

Agassiz contended that the embryo was superior to the adult and that, in

turn, the egg was more perfect than the embryo. This strange line of reasoning grew out of the necessity for explaining the presence of new organs in one of the four great groups of animals. Since the entire vertebrate group, for example, was related, such new organs as teeth, wings, lungs, etc., presented a difficult problem to the Creationist. Agassiz met this problem by attributing to the egg a complexity greater than that of the adult. Rogers took advantage of this unscientific proposition, thus placing Agassiz on the defensive. In the following manner Rogers carried his argument to fossil life:

As regards the statement that the most ancient types of life were higher or more perfect than recent ones, he had always considered Prof. Agassiz as maintaining that these earlier forms were of an embryonic character; and in this connection he remarked that the term 'perfection' is just as indefinite as the word 'species.' He considered perfection as specialization in each type; if an animal approach nearer perfection because, for instance, it be part fish and part reptile, or if a structure part animal and part vegetable be more perfect than the plant, then is the cell the type of perfection, combining as it does properties belonging to both kingdoms; he considered perfection, not the union of different types, but specialization in each particular type.

The recording secretary, Samuel Kneeland, indicated that: "Prof. Agassiz considered perfection to mean an embodiment of the highest combinations, the most complex representation of life. The embryo fish presents features of its type superior to those of the adult fish; the tendency to specialization increases with its growth, and the animal at last becomes only a fish, losing its embryonic type of the higher vertebrates. As a generalization or philosophic conception, the vertebrate egg is superior to man himself, inasmuch as it embodies all that may be produced from it (27).

Thus the first meeting was concluded. Never before had Agassiz met an

opponent who was his equal as a scientist and his superior as a logical thinker. He was annoyed when members of the audience interrupted him with questions or shook their heads in disapproval. These minor irritations were something that the great Louis Agassiz was unaccustomed to, and may account for some of the loose statements which led to his downfall—a defeat clearly foreseen at the end of the first day's arguments (28).

Agassiz was a poor debater, and often lost patience as this incident reveals. There was a Scientific Club consisting of several members of the Harvard faculty which held frequent meetings. At one of these meetings Asa Gray argued so pointedly against Agassiz that he became sufficiently angry to challenge Gray to a duel (29). These two men also encountered each other in arguments at the meetings of the American Academy of Arts and Sciences, and we note that Gray's retorts were given extensive recognition in England (30).

The Second Meeting, March 7, 1860

The Vice-President was in the chair. Mr. C. H. Hitchcock explained his map of the principal features of the complicated geology of the State of Vermont. Professor Rogers discussed the new facts revealed in Hitchcock's map, and asked permission to incorporate into the minutes a paper "On the Geological Structure of Western Vermont," which he had read at the American Association at Albany in 1851. The reading of these papers was followed by the presentation of a section of a tusk of an elephant and an explanation as to how it was formed; after which Rogers demonstrated the laws of fracture. The above incidents are recorded as indications that Rogers might have been ready to allow the question of Darwinism to rest. This, however,

was not what Agassiz desired. He had come to this meeting with a carefully-prepared paper on consecutive faunæ and their geological formations. He objected to the argument from "domestication" as an explanation of similar changes in geological ages, and argued that representatives do not pass from one fauna to another. He presented his own definition of faunæ as:

... groups of animals enclosed within circumscribed areas; there are many of these on the globe, and they must not be confounded with zoological realms; of the latter, New Holland may be mentioned as an example, having animals of a peculiar type; so are the East Indies, Africa south of the Atlas Mountains, America from the sub-arctic regions to Patagonia, and the arctic regions themselves. Faunæ, on the other hand, occupy more limited provinces characterized by species related to each other, as they are more largely in realms. Faunæ differ in various parts of the world, and no one can be taken as a type of existing creation; for instance, the fauna of Canada differs entirely from that of Africa, and any zoologist who should take one or the other or any single fauna as the type of the world's animals would commit an absurdity; yet geologists do this constantly in their identifications of geological periods, and of course fall into the gravest errors. He found fault with the methods of determining the limits of successive faunæ usually pursued by geologists; he thought that this order should be determined by the fossils; that the rocks should be regarded merely as the tombs of the fossils, that naturalists should try to find out the animals of an epoch, and establish the limits of faunæ on zoological and not on physical principles (31).

This gave Professor Rogers his opportunity; and he took full advantage of it. The question was: "Did species pass from one strata to another?" Before this line of reasoning presented by Agassiz could be accepted, the entire severance of these faunæ must be demonstrated. What were the facts?

In New York, out of more than seventy forms found in the strata below the upper limit of the Black River limestone, only three have been observed by Prof. Hall to pass up into the overlying Trenton

limestone, and on the same horizon a transition almost as abrupt shows itself in parts of Pennsylvania and Virginia. Here then we would seem to be justified in drawing a strong line of separation between the contiguous Black River and Trenton faunæ. But turning to Canada, we find a very different distribution of the fossils. In this region the Black River limestone, that is, the rock containing the characteristic Black River fossils, includes a preponderating number of species found also in the Trenton. According to the Canada paleontologists, fifty-two out of seventy-five are common to both formations, and what is still more interesting, some Trenton species are found in the yet lower group of the Chazy. Here obviously we can no longer draw a limit between the Black River and Trenton faunæ, but must blend them gradationally into one (32).

Seeing, then, that faunæ are not unfrequently mingled in contiguous formations, that they do not hold the same precise geological level or vertical distribution at different localities, that they may even become inverted in relation to each other, offering in this and other cases evidence of emigration and remigration in successive times, Prof. Rogers maintained that the *precise and absolute limitation* of faunæ to formations, as advocated by Prof. Agassiz, if true in any case, is at best but of local and partial application, and can not be the basis of a paleontological arrangement of formations. . . . In regard to the discrimination of species, the question at last must come to this: What is the limit of specific difference? who shall be the arbiter? what the principle of distinction between species and variety, and what the guide in drawing the lines of demarcation of the successive faunæ?

Prof. Agassiz remarked that he did not expect the immediate reception of his views, though convinced that they were true, but believed that after mature examination of his facts they would be generally received (33).

Agassiz then took an illustration from chemistry, and Rogers again turned the argument against him:

He alluded to chemistry, in which there was a time when platinum and other silver-like metals were not distinguished from silver; but in the progress of science they were ascertained to be separate and distinct species.

Prof. Rogers replied that this argument would answer equally well for the other side of the question; for instance, chemistry has reduced to one many supposed different species, as the diamond, plumbago, and carbon (34).

The meeting then turned to examine an exhibition of forty Brazilian birds; and, later, to elect new members to the Society.

The Third Meeting, March 21, 1860

The third meeting, on March 21, 1860, opened with President Jeffries Wyman in the chair. The first communication was a description of the color of the inside of fresh-water clam shells. In the two previous meetings, the arguments raised the important question of the stratigraphical relations of deposits formed in an ocean. Rogers gave his views under "stationary," "subsiding," and "rising." The critical manner in which Rogers met the argument of Agassiz places this debate in the front rank of scientific evolutionary discussions.

Both Agassiz and Rogers should have been familiar with Lyell's ideas on this subject, as he had phrased them, in 1842, in this way:

But if the bottom be lowered by sinking at the same rate that it is raised by fluvial mud, the bay can never be turned into dry land. In that case one new layer of matter may be superimposed upon another for a thickness of many thousand feet, and the fossils of the inferior beds may differ greatly from those entombed in the uppermost, yet every intermediate gradation may be indicated in the passage from an older to a newer assemblage of species (35).

Professor Rogers revealed that he was entirely familiar with this problem. In fact, Merrill (36) paid tribute to the excellence of the Rogers brothers in their work on fundamental problems relating to the physics and structure of mountain building. Evidence that the question of subsidence was being discussed prior to the Agassiz-Rogers debate, can be seen in the abstract of a paper on the subject read before the Montreal meeting of the A.A.A.S. by Professor G. H. Cook (37), of New

Jersey. Even as early as 1840, J. D. Dana offered a solution to the question of continental uplift and depression.

The following is a sample of Rogers's argument:

In the first and second of the conditions here named, the level of the resulting land would be *approximately horizontal*; while in the third case, that of the uplifting of the ocean-floor during the accumulation of the deposits, the surface would present a slope descending from the oldest deposits on the first shore-line to the strata latest formed; in other words, the *older deposits* would crop out at the *higher level*, and the successively later ones at a less and less elevation.

The Appalachian strata embraced between Lake Ontario and the Pennsylvania coal region present a relation of levels *the reverse of that last named*, the older strata cropping out at successively lower levels as we proceed northward, while the newer formations, the Devonian and Carboniferous rocks on the south, are piled up to a height of some thousands of feet above the level of these outcrops. For this and other reasons, Prof. Rogers could not admit the theory which regarded the present stratigraphical features of this region as evidence of a deposition of the strata during a long-continued upward movement of the ancient sea-floor (38).

It is interesting that the debate should finally turn to the Catastrophic Theory of Cuvier, a view that had been widely accepted. Within a few weeks after this meeting, Rogers presented a direct challenge to this theory of fifty years' standing in his study of the denudation of rocks:

This existing configuration has undoubtedly been the work of subsequent denudation, of which extensive and unmistakable evidences are apparent throughout the paleozoic area. The theory of an uplifting movement during the deposition does not, as has been supposed, dispense with the necessity of such a further agency for remodelling the surface. On the contrary, in this case, the depth of denudation required to carve out the profile of the region in question, so as to make it conform to the existing features, would be far greater than would be needed to bring the imaginary subsidence-area to a like agreement. In the latter conditions, the denuding force would be called on to remove only a certain amount of material

below the horizontal surface over the northern portion of the tract; in the former, it would have first to cut down the greatly elevated outcrops at the north to bring them on a level with the southern deposits, and after this to do an additional amount of excavation equal to that of the other surface (39).

Agassiz, on his part, displayed a lack of first-hand knowledge. The only reply he made was to re-state his conviction that "there was not subsidence during the deposition of the New York strata, and that the facts do not indicate it, but rather an upheaval" (40).

The meeting then listened to a letter from Liberia, Africa; but when this was finished, Agassiz immediately returned to the argument and attempted to answer Rogers's statements on migration.

His object at the present time was not to explain the origin and connection of faunæ; we must take them as we find them, as matters of fact, without reference now as to how they were produced. It is important in the discussion of this subject to bear in mind that some faunæ are strictly defined, while others run together; there is very great difference in this respect; Mr. Wallace, a strong advocate of Darwin's theory, admits the remarkable limitation between the Australian and Indian Archipelago faunæ, separated by a strait only fifteen miles wide, yet, with the exception of a few birds, entirely distinct. Faunæ are not necessarily, therefore, like each other because near together, nor unlike because widely separated; the former is shown by the case just cited, in which there is complete distinction, though circumstances favor a mingling of faunæ; on the other hand, those of widely distant Africa and the east coast of America between the tropics are very much alike. These do not look like migrations, which are at best limited, and in which, if the conditions of life were much changed, the animals would be destroyed; marine animals, in an element which invites migration, are very much circumscribed within limits as to depth of water, and could not migrate from one part of the world to another across ocean abysses. Another obstacle in the way of migration is the transfer of progeny; eggs in most animals cannot bear much change of temperature or of location, without destruction of the contained embryo. . . .

In regard to the vitality of eggs, the President [Wyman] remarked that it is well known that the eggs of salmon and trout are sent by *diligence* all over

France; and Rogers observed that the flight of most birds would enable them to multiply on both sides of a narrow strait like that alluded to (41).

The Fourth Meeting, April 4, 1860

The fourth meeting was held on April 4, with President Wyman in the chair. Agassiz opened the proceedings with the statement that he did not see evidence of subsidence and denudation, as suggested by Rogers.

He exhibited a series of fossils to show the distinctness of faunæ, explaining why it is not always correct to identify geological periods by the identity of fossils; two questions are involved in the examination of this subject, one that of time or of period, the other that of space or limitation of faunæ.

Preliminary to the principal topic, he stated that he knew no such thing as a variety in the animal kingdom, except such as are stages of growth, within the limits of species; he instanced as an example one of the meandrine corals (*Monicina*), and other polymorphous types, which come within this law; in 1200 echini which he had examined and carefully studied, he had not found a single variety which did not arise from an imperfect stage of growth; so in 6000 fishes, he had not seen a variety except in coloration, which he had before shown was connected with their growth. So that he would start with the propositions that animals do not vary, and that species remain within the limits of their type (42).

Rogers repeated and extended his arguments of the previous meeting:

Thus, therefore, on no hypothesis of a *secular rising* of the sea-bottom can we explain the formation of our Appalachian paleozoic deposits. On the other hand, considering their aggregate thickness, as well as their continuity, composition, and stratigraphical arrangement, we are entitled to conclude that they were accumulated during a *long period of subsidence of the*

ocean-floor, varied by many and long pauses and upward oscillations (43).

Agassiz's reply must have been made under emotional stress, for he conceded upheaval of the shore, though he refused to acknowledge denudation:

Prof. Rogers replied that he had listened with extreme surprise to the statement just made by Prof. Agassiz, disclaiming the theory of the rising of the ocean-floor during the formation of our northern paleozoic strata. According to his recollection, the discussion was commenced by Prof. Agassiz's denying the correctness of the views of Darwin and others of the extensive destruction of strata and their fossils during a period of slow upheaval, and urging as an insuperable objection the great extent and completeness of the paleozoic series of New York, which he maintained had been deposited during a *period of upheaval*. As, however, Prof. Agassiz has now stated that he recognizes the *subsidence* of the ocean-bed as essential to the theory of their formation, Prof. Rogers thought it of no importance in this connection how that depression may have been brought about, or whether it was accompanied by a stationary or a rising condition of the ancient shore (44).

Such is the record of the conclusion of this debate between Louis Agassiz and William Barton Rogers in the *Minutes* of the Boston Society of Natural History.

One naturally wonders how this debate influenced public opinion. A search of the Boston newspapers issued during January, February, March, and April of 1860, has thus far failed to show that it was even mentioned.

The author will welcome any criticisms or additions before this paper becomes incorporated into a book on the history of biology in the United States.

REFERENCES CITED

1. PERRIER, EDMOND. *La Philosophie Zoologique* avant Darwin. (Paris, 1896), 130. This account of the Cuvier-Saint-Hilaire debate was kindly translated from the French by Professor A. S. Patterson, of Syracuse University. See also: Biographical memoirs of Geoffroy Saint-Hilaire in the *Smithsonian Report*. On pages 161-174 (1861), M. Flourens gives an excellent account of the controversy between Cuvier and Saint-Hilaire. In 1862 (pages 384-394), M. de Quatrefages tells more of his personal history and lists his writings. A memoir of Cuvier is to be found in the *Smithsonian Report* (Washington, 1868), 121-140.
2. PERRIER, 129.
3. *Ibid.*, 131-132.

4. MARCOU, JULES. Life, Letters and Works of Louis Agassiz. (*New York and London*, 1895), II, 107.
5. MARCOU, I, 44-45.
6. *The Asbenaum* (*London*, 1860), II, 26.
7. *Ibid.*, 26.
8. WARD, CHARLES HENSHAW. Charles Darwin: the Man and His Warfare. (*Indianapolis*, 1927), 310; THOMAS HENRY HUXLEY. Man's Place in Nature. (1863), 114; LEONARD HUXLEY. Life and Letters of Thomas H. Huxley. 194, mentions the *Natural History Review* (1861), on page 194.
9. The account of this meeting is to be found in the *Asbenaum* (1860), 65. A vivid account is also given in Life and Letters of Thomas H. Huxley. (*New York*, 1901), I, 195.
10. WARD. Charles Darwin: the Man and His Warfare. 310; HUXLEY. Life and Letters of Thomas H. Huxley. 193.
11. Chambers Encyclopaedia. (J. H. Lippincott & Co., *Philadelphia*, 1893), X, 654. Samuel Willberforce, born Sept. 7, 1805, was created Bishop of Oxford in 1845. He was a man of charming manner, a gifted speaker, and a good executive. Through the fact that he was "too clever, too self-reliant, too persuasive, too fascinating in manner, too fertile in expedients . . . too facile . . . he got the sobriquet of 'Soppy Sam.'"
12. DARWIN, FRANCIS. [Editor.] Life and Letters of Charles Darwin. II, 115. Quoted from Lyell's *Letters*, II, 335.
13. *Gray Correspondence*, Gray Herbarium (*Cambridge, Massachusetts*): J. D. Hooker to Asa Gray, July 5, 1860.
14. ROBERTS, JOSEPH K. William Barton Rogers and his Contribution to the Geology of Virginia. *Proceedings, Geological Society of America* for 1935 (June, 1936), 306, 308.
15. DARWIN, FRANCIS. [Editor.] Life and Letters of Charles Darwin. (Appleton's Edition), II, 85.
16. ROGERS, MRS. EMMA SAVAAGE. [Editor.] Life and Letters of William Barton Rogers. (*Boston and New York*, 1896), II, 17-25.
17. *Ibid.*, 25.
18. *Proceedings, Boston Society of Natural History* (1861), VII, 231.
19. *Ibid.*, 232.
20. HUXLEY, THOMAS HENRY. *American Addresses*. (*New York*, 1877), 33.
21. *Ibid.*, 38.
22. *Proceedings, Boston Society of Natural History* (1861), VII, 232, 233.
23. *Ibid.*, 233.
24. *Ibid.*, 233.
25. *Ibid.*, 234.
26. *Ibid.*, 234.
27. *Ibid.*, 234-235.
28. MARCOU, JULES. Life, Letters and Works of Louis Agassiz. (*New York and London*, 1895), II, 109.
29. *Ibid.*, 110.
30. *Proceedings, Boston Society of Natural History* (1861), VII, 241-2.
31. *Ibid.*, 241.
32. *Ibid.*, 242-243.
33. *Ibid.*, 244.
34. *Ibid.*, 245.
35. LYELL, CHARLES. Principles of Geology. Seventh Edition (*Boston*, 1842), I, 296.
36. MERRILL, GEORGE PERKINS. The First One Hundred Years of American Geology. (*New Haven*, 1924), 663.
37. COOK, G. H. On the subsidence of land on the sea coast of New Jersey and Long Island. *Annual of Scientific Discovery* (*Boston*, 1858), 352.
38. *Proceedings, Boston Society of Natural History*. (1861), VII, 246-7.
39. *Ibid.*, 247-248.
40. *Ibid.*, 248-249.
41. *Ibid.*, 251-252.
42. *Ibid.*, 271.
43. *Ibid.*, 273-274.
44. *Ibid.*, 274-275.



FORM AND FUNCTION IN THE SLOTH

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INTRODUCTION

SPEED, speed and still more speed'' began a newspaper editorial recently, considering the impulses of civilized man. Regarding simple rate of physical movement, however, the distance-in-time curve for man and most of his interests has now become rather flattened at the higher levels. It may be interesting to observe in contrast a lowlier form, but one still in our own mammalian class, the proverbially tardy sloth. Its curve of activity, after many aeons of concentrated specialization, has become almost asymptotic at a very low level. But withal its biological restrictions the sloth has achieved in some ways much freedom.

The opening of an inter-American highway through Panama will allow the 60-miles-an-hour motorist to meet the 6-hours-a-mile sloth. It will be one of the most unique creatures to be found in the tropics. Loafing lazily in nearby trees, or crawling occasionally with many pains and much difficulty across the road, this blissfully inhibited tardigrade may prompt a refreshing and rewarding pause. It will furnish an amazing object lesson in leisurely living.

Almost wholly the three-toed species will thus be observed by the roadway, for the two-toed animal gives the deadly *Homo* a wide berth. The deep curiosity and normal absence of fear which are shown by

the three-toed *Bradypus* lead it into strange highways and byways in life. Somewhat like the inquisitive and voracious opossum, it may now and then be found almost within the precincts of one's culinary quarters. Yet relatively few people to date, even in the tropics, have met the humble sloth. On a well-travelled tropical highway, however, there will soon occur a great loss by slaughter of these animals—totalling many more than were ever consumed by the hungry native or utilized by the zealous scientist. Happily their great number and relative inaccessibility in the forest will prevent extinction of a highly interesting and edifying mammalian form.

HISTORICAL

Early accounts of the sloth are given by a number of writers, although they interest one more often by their quaint description than by factual exactness. One of the most interesting and apparently the earliest reference is that of Oviedo y Valdés (1526). Following several visits to many parts of the Americas, and gold-smelting operations in San Domingo, this Spanish knight and historiographer contributed classical and fairly trustworthy accounts of his travels. His book issued in summary form in Toledo over 400 years ago represents his first published natural history of the Indies, and from it the following delightful account of the sloth is derived.

[The author is greatly indebted to Professor Julio S. Galban of the University of Virginia for the translation here given from Oviedo's rare "Historia," in the University's Tracy McGregor Library. It may be observed that an effort has been made to retain the spirit as well as the letter of the author, in making the translation.]

Little Quick Pedro is the stupidest animal that can be seen in the world. So slow and heavy is he that it takes him all day to go fifty paces. The first Christians who saw this animal (remembering that in Spain the negro is usually called John White, so that it may be understood conversely) as soon as they set eyes on him gave him the name opposite to his nature: because he was extremely slow, they called him quick. This is one of the strange animals, very much seen in the mainland, and very different from all other animals. He must be as long as two spans when fully grown; very little more than this measure if somewhat over-grown: any smaller ones that are found are young. They are almost as broad as long; and they have four thin feet, and on each hand and foot four long nails, like those of birds, and joined: but neither the nails nor the hands are such as he can support himself on them, and because of this, and because of the slowness of his arms and legs and the weight of the body, he carries his belly almost dragging on the ground. His neck is high and straight just like a pestle of equal width to the end, without making any difference in width between the head and neck; and at the end of that neck he has a face almost round, very similar to that of an owl, and the hair itself makes a ring around his face, a little longer than wide; and his eyes are small and round, and his nose like a monkey's, and his mouth very small, and he moves his neck from one side to the other as if astonished; and his intention, or what he seems to try and desire the most is to hold on to a tree, or anything that he can climb, and so most of the times that these animals are found they are taken in trees, on which climbing very slowly they go clinging with their long nails. Their hair is between light and dark, almost the very color of the hair of a weasel, and they have no tail. His voice is very different from that of all the rest of the animals of the world: because it sounds only at night, and as a whole, in continued chant, from time to time, singing six notes one higher than the other, always descending: so the highest note is the first, and from that one he descends, lowering his voice, as one might say, *la sol fa mi re do*, thus this animal says *ha ha ha ha ha ha*. Without doubt it seems to me that, as I said in the chapter of the Armadillos, these animals might have been the origin or hint to make the armour of horses; so, hearing this animal, the first

inventor of music could have had a good base to give it beginning, better than any in the world, because the said Little Quick Pedro teaches us by his six notes the same as can be understood by *la sol fa mi re do*: returning to my story, I say that after this animal has sung at short intervals, he sings the same thing again. This he does at night and never in the daytime, and because of this and because he is near-sighted it seems to me that he must be a nocturnal animal and a friend of darkness. Whenever Christians take this animal, and bring him home, he goes around at his own gait; and neither by threat, blow, nor prodding does he move any faster than he is accustomed to do without tiring: and if he encounters a tree he goes to it and climbs to the highest of the branches, and remains in the tree, eight and ten and twenty days, and it cannot be known or understood what he eats. I have had him at home and what I was able to understand of this animal is that he must sustain himself on air; and of my opinion I found many in the land, because he has never been seen to eat a thing but continuously to turn his head, or mouth, towards the wind, more frequently than to any other part, by which it is known that the air is very agreeable to them. He bites not nor can he do so, since his mouth is extremely small, nor is he poisonous; nor have I ever until now seen an uglier animal, or appearing as useless as this one.

The illustration of the three-toed sloth from Oviedo's history (Fig. 1) represents the animal as if placed on the ground in a sitting posture like that assumed by a young child. This unique attitude is one which the animal may to be sure maintain momentarily: in any case it is true that the sloth presents an extremely quaint picture whether viewed sedant or scandent.

One of the early buccaneers, Exquemelin (1678), recounts that a Captain Sharp and his crew caught a sloth on a small island (the Isle of Gorgona or "Captain Sharp's Isle"), and commented that it was a beast "well-deserving that name."

Captain William Dampier's travels around the Bay of Campeachy and other parts brought him into contact with the humble sloth. Some of the animal's habits are described interestingly, with

not unusual over-emphasis. In his "Voyages" (1697) he remarks that

"They are very mischievous to the Trees where they come. . . . They never descend till they have stript every Limb and Bough, and made them as bare as Winter. It takes them up eight or nine Minutes to move one of their Feet three Inches forward; and they move all their four Feet one after another, at the same slow rate; neither will stripes make them mend their pace; which I have tried to do, by whip-

It resembles a middling monkey, but of a wretched appearance, its skin being of a greyish brown, all over corrugated, and the legs and feet without hair. He is so lumpish, as not to stand in need of either chain or hutch, for he never stirs till compelled by hunger. . . . The food of this creature is generally wild fruits; when he can find none on the ground, he looks out for a tree well loaded, which, with a great deal of pain, he climbs: and, to save himself such another toilsome ascent, plucks off all the fruit, throwing them on the ground; and to avoid the pain



FIG. 1. PROBABLY THE OLDEST PICTURIZATION OF THE THREE-TOED SLOTH (OVIEDO Y VALDÉS, 1526)

The unsupported sedant position is really an impossible one for the sloth, and the not unusual anthropomorphic representation is evident.

ping them; but they seem insensible, and can neither be frighted, or provoked to move faster" (Masfield edition, 1906).

The comments of Don Juan and de Ulloa on the sloth are more fanciful. These Spanish sea-captains, it may be recalled, visited the New World in 1735. A short excerpt is taken from the translation of their work (1748) by Adams (1807):

of descending, forms himself into a ball, and drops from the branches. At the foot of this tree he continues till all the fruits are consumed, never stirring till hunger forces him to seek again for food.

Buffon (1766) has described the broader features of the anatomy of sloths, including the stomach and intestines, sex apparatus, teeth and bones, as well as many external characteristics. He also remarks

that the Marquis de Montmirail kept a two-toed sloth for three years in a menagerie, and that it fed on bread, apples, milk,

Interesting observations have also been made by Oliver Goldsmith (1825). An animal that is slow from necessity, he



FIG. 2. A RATHER LIFE-LIKE ILLUSTRATION OF THE TRIDACTYL SLOTH FROM PENNANT (1771)

and "poisonous leaves." The illustrations by Pennant (1771) and by Buffon (1776) are rather imaginative (Figs. 2 and 3).

remarks, the sloth may move three feet an hour when impelled by the severest stings of hunger. He considered it represented an unfinished production of nature, the

"meanest and most ill-formed of creatures that chew the cud."

Remarking on the sluggardy of the sloth, Cuvier (1837) explains it is "because of a construction truly heteroclite." Nature, he says, seems to have amused herself by producing something imperfect and grotesque.

Some recent engaging articles on sloths have been written by Beebe (1925, 1926). Observing that it lives at a low ebb, or in low gear, the personification of deliberation, he adds that the sloth would be a fitting inhabitant of Mars, where the year is six hundred days long; self-centered and sub-reptilian in mentality, in a "perpetual estivation of sorts," it had no right to be living on earth. Probably about the lowest in its scale, as to touch, taste, sight and hearing, it was nevertheless better off, olfactorily speaking, than man. Many interesting habits and activities of sloths are described by Beebe, and several anatomical facts are given. Jaguars and wild cats, coatis, the anaconda and the harpy eagle are listed as enemies which at least occasionally eat sloths.

In a number of recent contributions, Wislocki has dealt with the important anatomical aspects of sloths; these are referred to in detail later. Extended bibliographies are given by this writer, and also by Beebe (1926). Other articles in the literature on the sloth are appropriately referred to herein, but no attempt has been made to give a complete bibliography. Most of the data contained in this review are, it may be said, derived from the writer's own records of experimental work carried out during several expeditions to the tropics. In nearly all cases observations were made on the commoner Panamanian sloths, the two-toed *Cholepus hoffmanni* Peters and the three-toed *Bradypus griseus griseus* Gray.

Three expeditions to Panama were made by members of the Department of Physiology of the University of Virginia Medical School in 1937, 1938 and 1939. Members of these expeditions besides the author were Mrs. S. W. Britton, Dr. Murray Brown, Mr. W. E. Atkinson and Mr. Raymond F. Kline. To these workers credit is due for much of the information contained herein, as indicated in separate scientific reports under their authorship. The author worked under the terms of a John Simon Guggenheim Memorial Fellowship during the years



FIG. 3. AN IMAGINATIVE, PLAYFUL SCENE OF YOUNG SLOTHS PICTURED BY BUFFON (1776)

1937 and 1938. Work was carried out in the first two years chiefly at the Institute for Research in Tropical America at Barro Colorado Island and surrounding territory, with the splendid help of Mr. James Zetek, Curator. Here it was possible to live with large colonies (50 to 100) of sloths, imported from the mainland, and observe very intimately their living habits. In 1939 investigations were undertaken at the Gorgas Memorial Laboratory, and from there field trips were made, with the invaluable co-operation of Dr. Herbert C. Clark, Director of the Labora-

tory. The author is much indebted to Mrs. Britton for the drawings contained herein.

CLASSIFICATION AND ANTIQUITY

Sloths may be designated briefly, zoologically, as of the mammalian subclass Eutheria, order Edentata, sub-order Xenarthra, and family Bradypodidae. In the two genera, *Bradypus* and *Cholepus*, several species have been described—*Bradypus infuscatus*, *B. griseus griseus*, *B. tridactylus*, *B. castaneiceps*, *B. ignavus*, *B. torquatus*, etc.; *Cholepus hoffmanni*, *C. didactylus*, etc. Differences in species appear to be highly variable and in considerable dispute, however, especially in the case of *Bradypus*. Four other distinct families also occur in the Edentates besides the Bradypodidae, namely the Manidae, Dasypodidae, Myrmecophagidae and Orycteropodidae. It should be said that the Edentates have been divided by some workers into the sub-orders Pilosa (including the sloths) and Loricata (armored Edentates).

Flower (1882) states that probably all the New-World Edentates, which represent by far the majority of the known species, sprang from one common stock in the Pliocene and Pleistocene periods, relatively late in geological history. In contrast, in his work on placentalia in the sloth, Wislocki (1927) remarks on the possibility of the great antiquity of the Xenarthra, including the sloths. The work of the present author also indicates that the sloth is a relic of a dim and ancient past. Some interesting connections of surviving sloths with the gigantic extinct Tardigrada (Glyptodontidae, Megatheriidae) have been suggested by some workers. According to Miller (1939), however, there is little or no conclusive evidence regarding the extinct forerunners of present-day sloths.

The term "sloth" was used to denote the animals described herein more than

300 years ago. Purchas (1613) writes that "The Spaniards call it . . . the light dog. The Portugals Sloth, The Indians, Hay." A further early reference is that of Crew (1681), who mentions "The Sloth. . . . An animal of so slow a motion, that he will be three or four days, at least, in climbing up and coming down a Tree." The two-toed sloth, *Cholepus*, possessing two toes on the fore-limb and three on the hind, also is given the common but still little-known name "unau," of South American (probably Tupian Indian) origin. *Bradypus*, or the three-toed sloth, having three toes on both fore and hind feet, is known commonly by the name "ai," an onomatopoeic term having reference to the shrill, bleating cry occasionally emitted by the animal, especially at night or when molested.

The delightful early Spanish term of ironical concept for a sloth is *perico ligero*, or nimble little Peter! By far the slowest and most typical of sloth-like animals, the antithesis of speed, are the three-toed Bradypodidae. The Cholepine two-toed sloths are in contrast much better grade or higher type animals; this is apparent from many physiological aspects, although they are still distinctly and properly classified as sloths. Some of the slowly-moving lemurs would almost certainly show functional correlations with the sloths, but zoologically they are widely separated from *Bradypus* and *Cholepus*. The sloth bear, sloth monkey, ground sloth and sloth animalcule are interesting extinct or present-day animals which are not included in the subject of this study.

Distribution

Sloths are found in the forest regions of tropical America from Honduras and Nicaragua in the north down through Panama and as far south as upper Brazil and Bolivia. They occur on both sides of the

Andes, a fact which earlier observers did not recognize. They are strictly limited to the New World, it may be emphasized, although several of the older historians indicate otherwise. It is nevertheless true that other animals inhabiting the Old World, such as African potto-lemurs and Asiatic lorises, have in the literature been popularly called sloths.

Bradypus occurs only in the lower neotropical altitudes, and is particularly prevalent in regions where the temperature is not widely fluctuating (in the heavily-wooded jungle depths). *Cholepus* also lives chiefly in the warm, tree-shaded lowlands, but is able to withstand the cold (possibly occasional freezing) of altitudes up to 7000 or 8000 feet. The latter form apparently does not extend farther north, however, than Costa Rica. Most species of *Bradypus* are distributed generally throughout the neotropics, although *B. castaneiceps* and *B. ignavus* have a more northerly distribution, and are particularly common in Panama and Costa Rica. *C. hoffmanni* is also commonly found in the latter places, as well as in Ecuador. *C. didactylus* inhabits chiefly Brazil and the Guianas. The largest sloths observed by the author have been those taken in Colombia. It appears likely from many considerations that these animals thrive best in the highly humid and wooded equatorial regions.

CHARACTERISTICS

General

In both genera of sloths and especially in *Bradypus* the head appears small for the body size. The broader snout and head in *Cholepus* are due in large measure to the extensive sinuses which are present. The external ears are very small and hidden in the hair; in *Bradypus* only a tiny pinna about 1 cm. across is present. The eyes are also small and round, and of a dirty

brown color. Passage through trees is obviously facilitated by the head arrangements.

Contrasted with the short neck of *Cholepus*, that of *Bradypus* is long and mobile, and along with the small head is suggestively reptilian. It is remarkable that the Bradypodine head may be rotated through 360° ; starting from the dorsal facing position a complete turn may be made. The fore-limbs in sloths are longer than the hind, which appears important in meeting the demands of arboreal life. In *Bradypus* the fore-limbs are longer, the hind-limbs shorter than the respective limbs in *Cholepus*; there is also greater mobility of the fore-limbs, which may indeed be drawn around to the back of the body, crossed, and returned forward to meet again over the abdomen. The hind-limbs of sloths (greatly shortened in *Bradypus*) serve a great deal of the time for maintaining hold or stance. A stumpy tail 8 or 10 cms. in length is present in *Bradypus*, while *Cholepus* is tailless.

Cholepus is much the larger, stockier-built animal, and is considerably less sluggish—under ordinary conditions it travels about twice as fast as *Bradypus*. Adult didactyl animals reach weights between 6.5 and 7.5 kgs., while the tridactyl form weighs between 3.5 and 4.5 kgs. The females are smaller by about 0.5 kg.

About as large as a small or medium-sized dog, therefore, sloths are markedly different in general form and appearance. The shaggy coat, long limbs and long curved claws, small head with bead-like eyes, and remarkably slow movement in the upside down position, set the animal apart from all other types. A very furry or hairy "teddy bear" indicates somewhat its general appearance (Figs. 4, 5, 9, 10), the young sloth especially resembling a ball of rather fluffy fur. For several months after birth the young possesses a



FIG. 4. THE TWO-TOED SLOTH (*CHOLEPUS HOFFMANNI*) IN VARIOUS POSITIONS

1 and 2, fighting; 3 and 4, nursing its young; 5, normal walking; 6, a bath before immigration check-up, on going north from Panama.



FIG. 5. 1, 2, 3 AND 4. THE THREE-TOED SLOTH IN TYPICAL POSITIONS, THE LAST-NAMED (4) A MALE WITH DORSAL SADDLE MARK; 5 AND 6. TWO WAYS OF DRINKING IN THE LABORATORY; 7. NATIVE BRINGING SLOTH IN FROM THE JUNGLE

soft, fine coat, and the three-toed form displays fur as an undercoat intermingled with coarse hair throughout life.

Bradypus is found, when shorn of its outer hair, to be beautifully marked with a black and white coat, somewhat leopard-like in character but with coarse linear mottlings of glossy black from 1 to 3 cms. wide. Both male and female three-toed sloths are thus observed to be marked when clipped. The male tridactyl animal gives a clue to this condition by its dorsal exposed white and black mottled area (in the older adult, yellow and black), some 10 by 15 cms. in extent, in the saddle position (Figs. 5, 4). This very distinctive dorsal marking has received no explanation, except to say that it represents a male sex characteristic. It begins to appear in males only a few weeks of age, and evidently the outer hair is then lost by slow degrees until the animal reaches about one year old, at which time it seems as if the area had been neatly plucked or clipped. Wislocki (1928) states that the beginning of a saddle mark is apparent in fetal male and female Bradypods, but that the male only develops the definitive mark at about the time of puberty. The condition may be reproduced in the female by shearing (Fig. 6, 1). In the two-toed sloth both under and outer hairy coats are similar in color and texture, and in this form there is no sex marking (Fig. 6, 3a).

Male and female sloths are difficult to distinguish, except for the dorsal marking in *Bradypus*. After long practice, slight differences in the urogenital area, indicative of the sex, may be detected.

In both genera, the long, coarse hair affords splendid protective coloring in the tropical foliage (Fig. 7). Patches or areas of different shades are very common. Various tints of gray are observed in *Bradypus*, while gray-brown (sometimes greenish-gray) usually predominates in

Cholepus. In the latter the coat is much less shaggy, and in its best condition it is indeed of a rather sleek, smooth appearance. The hair in *Cholepus* inclines back from the head and limbs and abdominal areas towards the mid-dorsal line and tail. In *Bradypus* also the hair exhibits this tendency, but is much more irregularly disposed and shows a frontal ruff, a central dorsal division and small shoulder and pelvic whorls (Fig. 8). In the case of both genera the hair arrangement undoubtedly allows optimal shedding of water, which is highly desirable in the (usually) very rainy sloth country.

In the didactyl sloth the hair under the microscope is found to be fluted longitudinally—the only known case of such mammalian hair markings (Fig. 11, A, A1). Exceptions are the vibrissae and fine hairs about the eyes, which are normally round and plain. From 8 to 10 grooves and columns, well rounded and the former with a tendency toward lateral hollowing-out, are found in cross-section in each hair; they run from base to tip, where all disappear uniformly. The three-toed sloth shows no such hair flutings, but transverse markings occur (Fig. 11, B, B1). In both forms the hair is scaly. Individual hairs appear under the microscope as white, yellowish, brown, gray, or black.

Different coat shades and ruff markings, and also skull contours and number of vertebrae, have influenced observers in designating "new" species. These characteristics are, however, highly variable in any small group of sloths collected in one locality, and the author sees no good basis for many of the species described.

Activities and habits

In the same order—the Edentates—with the aard-vark, pangolin and other divertingly interesting forms, the sloth presents an equally engaging cross-word puzzle to

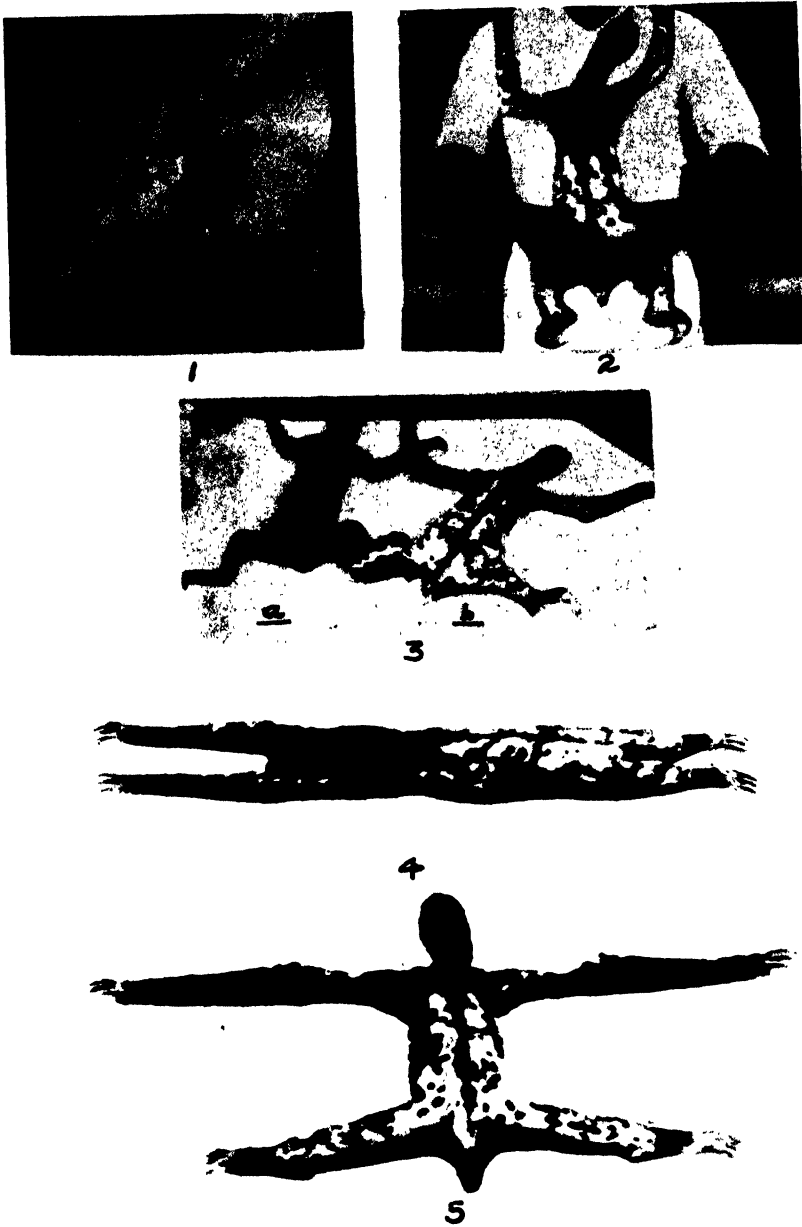


FIG. 6. MALE AND FEMALE SLOTHS SHORN OF OUTER HAIRY COAT, EXPOSING UNDER-FUR
 All are three-toed animals, except 3a, which is two-toed and of a uniform gray color. The black and white leopard-like mottlings in three-toed sloths are well seen in 1 and 2; in 4, the extraordinary streamlined form is observed, and in 5, the very long, slender limbs and extremely long claws are evident.

both naturalist and experimental scientist. "One more defect," wrote Buffon, "and it would cease to survive." But, while it is a defective creature, comments Beebe (1926), and a sloth in Paris would surely not long survive the pace, Buffon clinging upside-down to the branch of a tree in the jungle would expire even sooner! Spending most of its life in the mid-jungle trees, looking much like a hanging mass of gray-beard mosses, the sloth is wonderfully built for clinging and climbing. Nor-

slower than, those made head-foremost. Again, there is frequently no definite order of limb-movement maintained by tridactyl sloths, and one gets the impression that a "touch-and-go" style of progression is followed. In such an empirical way of travel, one movement is probably not dependent on or conditioned by that immediately preceding it so much as by the specific position of the body in space, which is modified from moment to moment by the swaying branches along

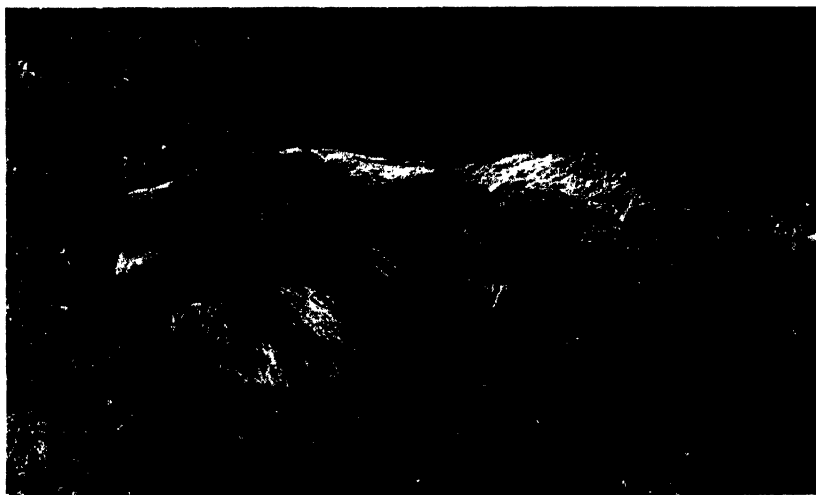


FIG. 7. THE SLOTH (THREE-TOED) IN A TYPICAL CRAWLING POSITION ON THE GROUND, AMONGST SOME CULTIVATED PANAMANIAN GRASSES

In the jungle trees and grasses the shaggy, patchy-colored hair is an even more effectual protective covering against detection.

mally, it travels on the under side of limbs in the inverted or back-down position, and shows very poor ability to progress in the upright position. While it usually advances head-forward, to be sure, the three-toed sloth may frequently pivot and go tail-first, while maintaining the same direction of movement, say along a branch or pole; and it may thus change about several times while traveling, in the course of a minute or two. Tail-forward movements are as fast as, or no

which the animal moves. Another influential factor is, of course, the proximity of food.

Sloths thus appear to possess an extremely limited sense of equilibrium. The upright position on all fours is seldom assumed under normal, active conditions, when the animal perches in tree crotches or comes to the ground. In the latter case progression is very slow (even for the sloth) and difficult; the spread-out or sprawling position of the body and limbs

indicates an undeveloped musculature (for this situation), and also demands no effort in balance. Although its home for the greater part has been made in the trees, the sloth has resisted to only a slight extent

appears to do most of the time, if one may credit the observations of hunters and laboratory workers.

In justice to the sloth, however, its normal mode of progression gives it easier



FIG. 8. YOUNG THREE-TOED MALE SLOTH, CLINGING TO VERTICAL WALL

The hair lines of limbs and back are typical, and the dorsal saddle mark is about one-half developed in this case

the influence of gravity, and covets the delights of dangling and swinging in space. With its remarkably long, curved claws, it is also well adapted for maintaining a fixed position with ease. This it

and surer access to pendant fruits and leaves on which it feeds. Only a slight development of attitudinal and equilibrational reflexes would appear to have been demanded. In the case of monkeys, the

usual upright or head-up position involves, in contrast, a much more compli- slip or even fall from the trees on which they are feeding, the sloth is in contrast



FIG. 9. SKETCH OF THE TWO-TOED SLOTH (*CHOLEPUS HOFFMANNI*) TAKING UP TYPICAL FIGHTING POSTURE WITH ARM RAISED TO STRIKE



FIG. 10. LIFE-SKETCH OF THREE-TOED SLOTH (*BRADYPUS GRISEUS*) CARRYING YOUNG ON BREAST, AMONGST *CECROPIA* FOLIAGE, ITS COMMON FOOD

cated set of reactions; and while these primates may occasionally be observed to the surer-footed and more specifically adapted animal for arboreal life.

Bradypus is a great sitter; the greater part of its life, perhaps four-fifths, appears to be spent thus, sleeping or dozing in the branches or smaller forks of trees, with

The higher trees are sought for rest when the foliage is thin, and the lower ones when the vegetation is dense enough for hiding. The stumpy tail helps consider-

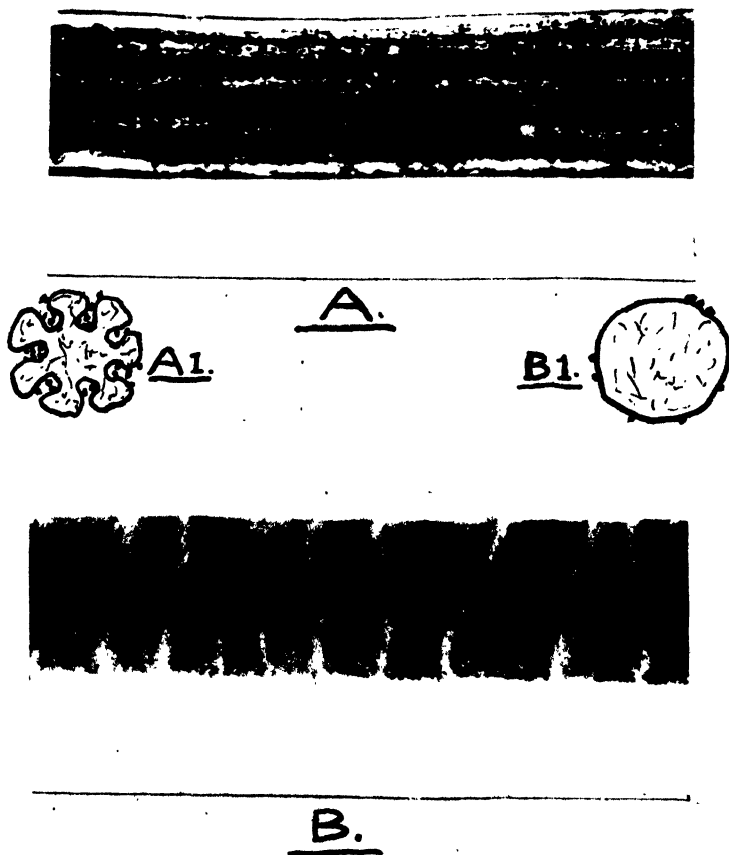


FIG. 11. MICROPHOTOGRAPHS OF TWO-TOED (A) AND THREE-TOED (B) SLOTH HAIR

*A*₁ and *B*₁ indicate the respective hair shapes in cross-section. The flutings in the Cholepine hair are unique amongst mammals. The great numbers of algae infesting the hair are evident.

fore-limbs often crossed over the breast and head tucked upon them. Notwithstanding this, and the fact that the sloth's stomach is always chock-full, it never accumulates any fat or "puts on weight"!

ably as a prop in providing the personal sitting quarters, and this is possibly correlated with the stunted and worn-down appearance of the caudal member.

Cholepus also spends a great deal of time

in the squatting posture, but rests occasionally in the upside-down position, suspended by all four limbs. Wislocki (1928) has stated his belief that *Cholepus* spends much of its time in the latter position, but the present writer could not confirm the point. In observations made in Panama on a large colony of sloths over a period of two weeks, at different times during the day, the two-toed variety was found when resting to maintain the upright clinging or squatting position in 85 per cent of the counts, and the three-toed animal in 90 per cent (Britton, unpublished observations). At other times the inverted, clinging posture was assumed. The rather unnatural conditions present in even a jungle laboratory would modify to some extent, however, the deportment of the sloth.

Habitat and travel

Commonly a particular neighborhood is favored by individual sloths for long periods at a time. In some cases an animal has been observed to remain even in the same tree for days or weeks. Favorite roosts in trees and thick foliage have often been observed. The alcabu or prickly yellow tree, possessing large spines on its trunk which defy climbers, appears to be a common resting place of *Cholepus*. Excursions for food are made particularly at night, when both species are most active. The Indians have a saying, however, that when the wind blows the sloth begins to travel—and in much of the sloth country the trade winds start at about 10 A.M.!

Movement is made from tree to tree via the ends of branches when possible (as it usually is in the thick jungle), but descent to the ground for passage may occasionally be made. While the more agile two-toed form is rarely seen on terra firma, *Bradypus* may be met fairly often on the highway or trail, and it sometimes approaches the out-

skirts of towns. Mating and parturition apparently occur on the ground in both species (see later).

Sometimes, distances of several miles may be covered in the course of a few days. The sloth is moreover a good swimmer, and may cross rivers or a mile or so of open water. The latter fact has been observed in the Gatun Lake area of the Panama Canal, where sloths fled from the islands about twenty-five years ago when the lake was formed. Today, these animals baffle all attempts to insulate them in this area by swimming to the mainland whenever they are released on even the larger islands, such as Barro Colorado.

There are indications that considerable numbers of sloths may move or migrate from one locality to another, several miles distant, in the course of a few years. Such changes do not appear to be related to food or climatic conditions, or to the larger animal enemies. Observations which have been made on this point have been limited, however, to the central parts of Panama, particularly to the Canal Zone where man has extended his activities rather rapidly, and they may possibly not hold for other areas.

In the jungle, sloths are usually found resting or travelling as solitary individuals. Many natives assert that if one sloth is discovered, however, another may be found not far away. In one very unusual instance, native workers near Cristobal sighted five three-toed sloths in different parts of one large tree. Both didactyl and tridactyl sloths may range over the same neighborhood together, while in other cases one genus may occupy an extensive area alone. In the case of long-confined animals under laboratory conditions, each genus may be observed congregating separately, in the heat of the day, in shady corners of the pen.

Males and females associate together in this way indiscriminately.

When first taken and placed in open-air cages near the laboratory, the sloth appears ill at ease and continually seeks a way of escape. Clawing of the cage and frequent sniffing of everything animate and inanimate within range are observed over a period of three or four days, after which time the animal settles down to an apparently normal, sedentary life.

Fighting propensity

When sloth meets sloth there is usually a fight, at least in the rather restricted quarters of the laboratory. Two-toed sloths are aggressive, and when approached will readily tackle almost any animal including man. *Bradypus*, however, is a poor fighter and never appears to pick a quarrel, but will strike back weakly when molested.

The fighting *Cholepus* usually holds on grimly by its hind-limbs to a branch or the cage wall, and lashes out fairly quickly with one or both long and dangerous forelimbs, while teeth are bared and the powerful jaws stand open ready to come together on any object with resounding clack (Fig. 4, 1, 2). An attempt is made to draw an adversary, when caught, towards the open jaws. The claws and teeth are formidable weapons, and even sloths themselves with their supertough hide may be badly scarred and torn in combat with each other. An inch pine board may be bitten through and splintered readily. The fore-limb flexion or striking movement of *Cholepus* is fairly quick, and has been called a "pugilistic short-arm hook" (Beebe, 1926); the preparatory extension component is, however, a slow, "wind-up" affair.

Tenacity to life

Wounds in both forms usually show clean, rapid healing, but deep injuries may

become badly infected. An amazing tenacity to life is shown by sloths in their ability to survive for long periods after extensive trauma, apparent drowning, or anesthetization far beyond respiratory failure. Beebe (1926) has mentioned for example that a sloth may survive immersion for 40 minutes in water—almost as long a period as the whale may spend submerged! In the writer's experience, recovery of an animal may also occur after suppression of respiration for 30 minutes by ether.

In some tropical areas the sloth has been used by natives for food, but the flesh is very tough and most difficult to strip of its hide. In other parts there are definite taboos, or "trafers" against killing the animal. Kahn (1931) remarks that individual natives may have particular traferes: thus, one may not shoot a sloth in Dutch Guiana, but if he should do so, his gun would be spoiled. Amongst native hunters it is rather generally considered to be unlucky to shoot or otherwise injure the sloth.

If one may make a rough approximation regarding age from observations on about 300 sloths in their native country, it would seem likely that these animals have a normal life-span of from 8 to 12 years, and may perhaps even live up to 15 years of age under optimal conditions.

Ability to learn

Although it puts up a weak resistance to capture in the jungle, *Bradypus* soon becomes docile and shrinking in the surroundings of the laboratory or garden, and may quickly become a pet. Colombian and other natives may now and then be seen travelling with such animals as pets clinging to their backs. *Cholepus* is tractable when young, but rather difficult to tame in adulthood. When kept in the laboratory for some weeks, however, it

tends to become fairly sociable. The earlier American workers on the Panama Canal collected sloths, among many other interesting forms, and hunters and others there today occasionally take the animals home to their gardens as attractions.

Some ability to learn or develop certain habits is shown, especially by *Cholepus*, after a week or two under laboratory conditions. Regular eating and drinking habits become established readily (Fig. 5, 5, 6), and food such as a banana may be eagerly sought after, and even delicately taken from one's hand. The appearance of the water boy signalizes drinking time, and turning on a faucet in the pen quickly attracts the thirsty individual. *Cholepus* has been observed to drink from a running water tap.

Fairly good responses are noted in training the sloth to travel on a horizontal bar or along a special track; also, when one makes frequent blood samplings from a vein, a certain adaptation of the sloth to such treatment is observed. Individual haunts in the pen are recognized and honored after animals have been in captivity for a few days. In the tropics both genera may be kept indefinitely under good conditions in the laboratory. In cooler latitudes also *Cholepus* lives well, but *Bradypus* is kept alive only by very careful diet and attention to environmental temperature.

Sloth parasites

Sloths afford harbor for an assortment of animal and even some plant life. The hair of both *Cholepus* and *Bradypus* is thickly covered with small green algae similar to the common parasite *Chlorococcum* (Fig. 11): *Bradypus* usually shows the greater infestation. Young sloths acquire the parasitic covering after they are a few weeks old. The algae are very densely packed, and occur irregularly or in

columns or chains, one to four in number wide, around the hair, in the case of the three-toed sloth with ordinary round hairs. Similar chains are found along the hair length, but in the grooves, in the two-toed animal with fluted hair. The dorsal parts are particularly well covered with algae. A rather bright green coloration is thus developed over the more exposed areas of the sloth, because of the algae infestation, in the wet season of the year. In the drier periods the algous covering tends toward a brownish-green hue, although a little water sprayed over the animal restores the brighter green tint.

Supporting this protective coloration afforded the sloth in its changing jungle environment may be noted the coarse, moss-like hair itself, strikingly similar to the surrounding masses of epiphytic vegetation. When these facts are coupled with the animal's very slow movements and tendency to secrete itself, sleeping hours on end, in the thicker foliage or angular, more inaccessible branches, the preservation coefficient of the sloth would appear to have been set at a high level. With such relatively passive or easily acquired and effective survival factors, the limited defensive ability of this tardigrade (especially *Bradypus*) and also its uniparous habit are in good biological harmony.

The sloth pelage, besides being covered with small algae, gives gracious refuge to several higher forms. Moths are at home in the hairy coat, small beetles have been observed, and ticks burrow through and into the skin to find their living. In the tropical laboratory, large cockroaches sometimes find a hiding-place and possibly food in the sloth hair. With rather generalized internal vermic infestations added to the list, the sloth takes first rank as a "buggy" animal. Several species of moths, ticks, and roundworms which infest the sloth have been described. A few

generally interesting facts on some of these parasites are given here.

Sloth moths are the only Lepidoptera known to be ectoparasitic in the adult stage. Three which have been described are of the family Pyralidae, and belong to distinct genera. The moths show great activity, scurrying about in the deep hair, as soon as the sloth is caught; if much disturbed they will fly off to a nearby perch, or settle on the intruder's hair, and then return to their host later. They do not appear to spend all their life in sloth

preen themselves, very little attention appears to be paid to the ticks, which are found on different parts of the body and sometimes attain a large size, some 2 cms. or so in diameter.

A small black insect, apparently a beetle and about 3 mms. in length, has been observed occasionally by Beebe (1938) and by the author in the commodious sloth hair. It does not appear to have been described in the literature.

Three or four different helminth parasites (Filariidae, Spiruridae, etc.) have

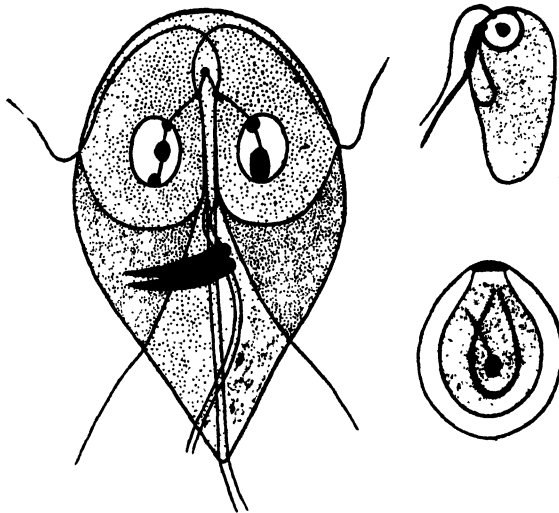


FIG. 12. SOME INTERESTING PARASITES FROM THE SLOTH INTESTINE (FROM HEGNER AND SCHUMAKER, 1928)

hair, however, since they have been taken in night-traps. Further, they do not seem to feed while on the sloth, since the mouth parts of all specimens examined have appeared coiled and atrophic. The larvae have apparently not yet been recognized but are possibly present, and may feed on fats on the sloth hair or on the abundant algae.

Four species of ticks have been described as infesting *Bradypus*, and apparently one or two species are found on *Cholepus*. Although sloths occasionally scratch and

been observed in sloths (Fig. 12). They occur in the stomach, mesentery, and other parts, sometimes in great numbers, and many appear to be peculiar only to the sloth. Again, the three-toed form would appear to be the greater sufferer; at least, most vermes have been observed in this animal.

Food

Voracious eaters under natural conditions, sloths apparently utilize many varieties of leaves and fruits for food. When

an animal is taken in the field, the stomach contents may be found to comprise more than a quarter of the body weight. The gastric sac is really amazingly large. Even under laboratory conditions, didactyl sloths consume large amounts of foodstuffs—bananas, oranges, figs, lettuce, hibiscus, and especially cecropia leaves. Tridactyl animals in captivity may usually be coaxed to take cecropia and hibiscus leaves, but sometimes refuse all food and succumb within a week or so. Raw beef was taken from the hand and eaten fairly readily by *Cholepus*, while *Bradypus* showed little interest in it. Both forms devour the placenta following birth of their young. Water is taken in fairly large amounts by lapping with the tongue, similar to a dog.

Mating, placentation, birth

Only one report of the apparent mating of sloths has come to the attention of the author. This was given by three bush workers in the Panama Canal Zone, who stated that they came across two animals of the two-toed species together in the tall jungle grass. They were locked in close embrace, ventre-à-ventre, the long claws of each embedded in the thick fur of the other, and almost certainly engaged in sexual intercourse, according to the witnesses. No signs of fighting were evident. Several general muscular spasms were said to have taken place over the period of about half-an-hour while the animals were observed. It may be said that although the sloth usually will scuttle away as fast as it can travel on the approach of man, not the least attention was paid in this case to the onlookers. It was found impossible to separate the animals by force, and they were left to their own devices by the usually kind natives. The ventre-à-ventre position in mating would appear to be demanded by

the anterior position of the genitalia and the forward-tilting pelvis.

Some cryptic comments have been made by Beebe (1926) on the mating of sloths, which he notes occurs in spring. The courtship, he relates further, is "unemotional, direct and brief."

Following the older work of Turner (1873), a number of observations have been made in recent years on placentation and the early development of sloths. Those of Wislocki (1927) and Heuser and Wislocki (1935) are very interesting and comprehensive. It is indicated by these workers that breeding may occur at any time of the year, but more often early in the dry season. Intrauterine development showed in numerous respects, particularly in the relations of body stalk, amnion and yolk sac, a striking degree of similarity to the corresponding developmental stages in man.

The hair lines in fetal sloths are said to be the same as in the adult, and the posture *in utero* is similar to that of the grown animal in sleep (Fig. 13). Fetus and adult alike retain masses of fecal pellets in the rectal pouch for long periods. The gestation period probably lasts between 4 and 6 months, Wislocki states, or considerably longer than that of cats and dogs.

Several sloths have been born in the laboratories set up by the author and his associates, both in Panama and in the more natural surroundings at Barro Colorado Island. Only in two cases, however, have the birth processes been observed from the beginning. These are recorded below.

Gorgas Memorial Laboratory, March 17, 1939.

At 1.20 p.m., the attention of Tom, the laboratory boy, was drawn to one corner of the pen, where a two-toed sloth was crouching and being teased by a group of chattering monkeys picking at it from the adjoining cage. The sloth made low groaning sounds occasionally, as it apparently experienced labor pains. It frequently stretched itself, and then drew

up into a ball-like mass. Presently a small amount of blood was noted about the urogenital opening. No other fluid appeared.

At 1.30, the top of the head of the baby sloth was observed at the opening, and ten minutes or so later the shoulders appeared.

At 1.45, the baby sloth was expelled fully enclosed in a rather thick, loose-fitting periderm or epitrichial membrane. The membrane invested all parts of the

the mother's fur, and in the near vicinity. Occasionally, tension on the cord held with the placenta by the mother caused the young one to cry out with a long, high-pitched squeal. Every little while the mother licked and fondled the baby, and also ate remaining fragments of the periderm. The mouth parts of the mother were covered with blood at this time.

At 2.05, the baby was very active. It was with-



FIG. 13. FETUS OF THREE-TOED SLOTH AT ABOUT TWO-THIRDS TERM, WITH CORD AND DIFFUSE PLACENTA ATTACHED

The hair has not erupted, and the epitrichial covering of the fetus has therefore not lifted. Note the small pinna and the extremely long fore-limb (6 cms.) compared to a total body length of 10 cms. The tail is relatively prominent at this age.

body like a garment and was not of the usual mammalian, amniotic sac-like formation. The umbilical cord was attached. Within a few moments the placenta appeared. After parturition, the mother quickly began to claw and chew the membrane, and the new-born sloth struggling vigorously at the same time caused its coverings to rupture further. A little later the mother chewed up the placenta, and began to swallow it in small fragments. The new-born sloth meanwhile began to crawl about on

drawn from the mother, upon which the latter displayed resistance and anxious concern. Several photographs were taken.

At 2.40, when the young one was returned, the mother again became very excited, and then showed considerable affection for the offspring. In a few minutes she again began eating the placenta, and soon had devoured it completely; later the cord was bitten off close to the baby's abdomen. The mother ate part of a banana, but was evidently

fatigued and soon fell asleep with its baby on its breast.

At 3.30, the weight of the young sloth was found to be 340 grams, and of the mother 3.97 kilograms.

The mother sloth became much disturbed every time its newborn was temporarily removed, running (sloth-like!) around the cage, clawing and biting at all objects and growling viciously. When given its young one again it immediately became quiet, and began licking and nursing it with great care. It also cleaned all its accessible parts by licking, giving special attention to the urogenital area.

Next day the mother sloth still retained the same corner of the large cage, carefully nursing its baby.

On another occasion (May 10, 1937) a two-toed sloth was born dead in the laboratory. It was enclosed in a thick epitrichial sheath, but no placenta was observed at the time. The young sloth weighed 398 grams.

The birth of one three-toed sloth has been observed. When the attendant noticed the mother, it

was in one part of the large cage alone, stretching and moving occasionally as if in weak labor. The top of the oncoming head had appeared at the urogenital opening; there was no evidence of blood or other fluid in the neighborhood. Within three minutes the young sloth was fully delivered, covered completely with the epitrichium. It struggled and cried, and the attendant slit the membrane and peeled it away, and also severed the umbilical cord and tied it. The remaining end of the cord was left extending from the urogenital canal. At no time during these procedures did the adult tridactyl animal show any maternal concern for its offspring. The newborn sloth, when placed near its mother, crawled quickly on to the latter's breast and began nursing. Later the mother was found to weigh 3.62 kilograms, and the young sloth 250 grams.

No placenta or cord was found in the pen some time afterwards.

The young one was kept with its mother for some time under laboratory conditions, and both did well.

(To be concluded)





THE SEX RATIO, FERTILITY, AND ANCESTRAL LONGEVITY

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THE proportion of the sexes within the family, tribe, or nation has long attracted man's attention. The fundamental desire for survival would alone have made the sex ratio an important question for reasons economic and martial. Added to this is the closely related wish to extend survival into the future through lineal descent. Some of the earliest writings indicate that such descent was believed to be through the males of the group, and fathers have, therefore, always put a premium on male offspring. It is no wonder that attempts to alter the proportion of sexes should have first found expression in theories concerning sex determination, and recipes for producing the desired sex at will. With the lack of knowledge concerning the anatomy and physiology of the reproductive system, ancient theories were purely products of speculation.

EARLY THEORIES OF SEX DETERMINATION

Hippocrates (460-370 B.C.?) [translated by Adams, 1849] believed that the male foetus was located in the right side of the uterus, and the female in the left. This was based upon the idea that the human uterus was bipartite. The theory was enlarged upon by Aristotle (384-322 B.C.) [English edition by Moritz and Chambers] who prescribed a course of procedure for begetting children of the desired sex.

The woman wanting a male child should lie on her right side after intercourse, in order that this side might be the place of conception, "for therein is the greatest generative heat, which is the chief procuring cause of male children." The method was said to fail only rarely, especially if the woman kept warm and with little motion, also drinking hissope and saffron in a glass of malaga. In order to have a female child the woman should lie on the left side and think strongly of a female, for Aristotle believed that imagination of the mother might often determine the sex. Galen (130-200 A.D.?) [translated by Daremberg, 1856] also thought that male offspring were formed as a result of greater heat. Not only did he believe that the male was formed in the right side of the uterus and the female in the left, but also that the right and left testicles of the father formed male and female children respectively. The difference in heat of the two sides was supposed due to greater vascularity on the right.

During Aristotle's time there were several other ideas concerning sex determination. He said that the best time for a conception to result in a female birth is in the wane of the moon while in Libra or Aquarius. He also mentioned the ancient physicians and philosophers as having said that the sex of the child is decided by the relative strengths of the

male seed and of the menstrual blood, but he thought this to be a fallacious theory.

The writings of Hippocrates, Aristotle, and Galen dominated thought for many centuries. Lemnius (1572) wrote what was representative of the knowledge of his time when he considered the uterus as a plowed field for the male seed to grow on. Whether the child would be male or female depended upon which side of the uterus the seed fell, the temperature, the time of year, and the amount of menstruation. This, it will be noted, is identical with views expressed almost two thousand years earlier. Some of these ideas have in some degree persisted to the present day.

It is well known that William Harvey (1578-1657) dared to dissent from the established ideas of the early Greeks, backing his statements with careful observation. Certainly Harvey knew that the human uterus was not bipartite, but he proceeded to test the application of the ancient theory to lower mammals. In his work *On Generation*, published in 1651, he speaks of detailed studies made on deer during gestation. "Males and females are met with indifferently in the right and left horn of the uterus. I have, however, more frequently found females in the right, males in the left horn; and I have made the same observation in does that carried twins, as well as in sheep. It is certain, therefore, that the right or left side has no appropriate virtue in conferring sex." Harvey also said that physicians of the time believed that the male and female both ejected their fluids into the uterus, and that the sex of the progeny depended upon predominance of one of the fluids. Highmore's (1651) writings (cf. Cole, 1930) are representative of this group. According to his theory, the blood stream collected particles from every part of the body, and these were carried to the genital glands where they

were concentrated into the germ. There were, then, two kinds of seed, male and female, sex being determined by a struggle for dominance at the time of conception. This also was an ancient idea, first postulated by Hippocrates [translation by Coxe, 1846]. He believed that although the male seed was the stronger, it would be suppressed by a greater quantity of female seed. Whichever ultimately predominated determined the sex. Aristotle said that the ignorance of the "ancients" caused them to fall into error on this point.

The invention of the microscope by Leeuwenhoek (1632-1723) resulted in wild flights of the imagination because of inaccurate observations due to crudeness of the earliest instruments. There arose a large group of preformationists who claimed to see a completely formed individual or homunculus within the egg or sperm. Highmore believed that the germ represented the substance of the body, but not its visible form. Buffon (1769) thought that organic particles from all parts of the body assembled in the germ cell in the same positions which they had within the body, and that sex was a matter of dominance of the male or female germ. Hartsoeker (cf. Cole, 1930) in 1694 assumed that each seminal animalcule contained a tiny foetus, and that each of these in turn held an infinite number of smaller animals of the same species, both male and female. Hence the sex of every individual was predetermined since the creation of the species. De Launay (1698) opposed this view, supposing that the germ of each parent held a small foetus of the same sex as the parent. Only one of these would survive to determine the sex of the child.

The preformation doctrine and sexual theories which accompanied it were die-hards, gradually succumbing only more

than one hundred years later because of their incompatibility with advancing knowledge of cell division and evolution. In the meantime the ancient theories of the Greek physicians and philosophers were undergoing a rejuvenation.

In 1786 Henke performed unilateral ovariectomies on pigs, dogs, and rabbits, claiming that subsequent conceptions yielded only males from the right ovary and only females from the left. This is a modification of Hippocrates' theory concerning the uterus. Later Seligson (1895) similarly operated on rabbits, arriving at the same conclusion as Henke. Dawson (1909) confirmed the hypothesis and elaborated upon it. Using as evidence clinical cases, he concluded that either testicle may result in both sexes of offspring, but that the right ovary produced males and the left females. The following year Doncaster and Marshall (1910) tested Dawson's work. Rats which had undergone unilateral ovariectomy were found to produce both males and females from the single remaining ovary, since autopsy later proved that there had been no regeneration of the removed tissue. King (1911a) further blasted the ancient theory. She made cross matings of hemi-spayed and hemi-castrated albino rats, all matings resulting in both sexes of offspring. There were 42 males and 41 females produced, a proportion very close to that of a normal rat population. Parker (1914) examined pairs of unborn pigs in the bifid uteri of the mothers. He found the sexes distributed as follows:

	♂♂	♀♀	♂♀
At division of horns of uterus...	252	240	456
Horn next to right ovary.....	228	209	434
Horn next to left ovary.....	216	208	447

Since it is extremely improbable that all of the males found in the left side had come

from eggs of the right ovary, and that the females in the right side had migrated from the left ovary, Parker considered this data as disproof of Seligson's work. As was pointed out by Marshall (1925), birds normally have only one functional ovary, and yet produce offspring of both sexes.

There have been several cases among women where a conception subsequent to the removal of one ovary has resulted in births of male progeny from the left side, or of females from the right. Rawlings (1922) cited a case in which a male was produced by an egg from the left ovary. It is obvious that the original hypothesis was a false one, and early experiments alleged to support it are now disregarded.

Other theories of sex determination arose to take the place of the time-worn idea that each ovary produced only offspring of one sex. Most of these were variations of the thesis that sex depends upon the time during the ovarian cycle at which the conception takes place. The studies relating to this subject will be discussed in a later section concerning the sex ratio.

Nutritional theories have often been propounded to explain sex determination and differential sex ratios. In his studies on *Hydatina senta*, Nussbaum (1897) said that if a female is well nourished shortly after emergence, she will later produce large eggs which develop into females. On the other hand, a poorly fed female will produce small male eggs. Some biologists believed that not the quantity of nourishment, but the chemical constituents of the food determined sex. The writings of Schenk (1902) are representative of this group. According to his theory, a diet high in carbohydrates fed to the mother before conception results in the birth of female children, whereas

a protein diet is responsible for males. The investigations of King (1907, 1909) on *Bufo lentiginos* did much to undermine the notion that sex can be determined by feeding. She found no significant difference between the proportions of sexes among normally fed tadpoles and among over-nourished tadpoles, nor did a protein or carbohydrate diet exert any influence in sex determination in the toad. Reed (1913) criticized nutritional experiments of Geddes and Thomson (1889) which were alleged to give positive results as being a contradiction to Weismann's ideas on non-inheritance of acquired characteristics. The basis of the criticism is that nutrition can at most result in temporary somatic modifications and hence cannot affect the offspring in any manner. This in itself does not disprove, however, that nutrition may have an influence on characteristics of the progeny subsequent to fertilization, especially in viviparous organisms. Nutrition is certainly not the dominant factor in sex determination, but its influence on the sex ratio still remains a moot question. In man the problem is not open to laboratory experimentation, so it has been approached by studying the proportions of sexes during wars and famines, and among different economic classes.

Superstitions have always had a large influence on the minds of people desiring a child of a certain sex. Økland (1932) discussed these at length. Two thousand years ago the idea started that phases of the moon determined sex, a figment that is not yet outworn. Another myth postulated that if conception was properly timed with the state of wind, rain, or temperature, one could have a boy or girl at will. Wishful thinking or temperament of the parents has had a prominent place in such superstitions. Passionate wives supposedly have male children, and

likewise vivacious wives and phlegmatic husbands. Primitive peoples perform ceremonial dances, while at one time Europeans buried perforated coins outside the door in order to have sons. Another bit of folklore held that the husband who had intercourse with his boots on would infallibly be blessed with an heir to his name. With the increasing education of the masses such superstitions have diminished. Even more plausible theories have been abandoned or have undergone radical changes as a result of important findings at the turn of the last century.

THE CHROMOSOME MECHANISM IN SEX DETERMINATION

The discovery of unequal sex chromosomes by McClung (1902) while studying spermatogenesis in *Xiphidium fasciatum* and in the Acrididae generally, inaugurated a new era of thought concerning sex determination. The chromosome mechanism is adequately described in a number of books on genetics. For the present section general references have been made to Lindsey (1932), Sinnott and Dunn (1939), Waddington (1939), Marshall (1925), and Sturtevant and Beadle (1939). Within the body cells and primordial germ cells of an organism there are found like pairs of chromosomes. The exception to this is in the sex chromosomes or allosomes where the members of the pair are dissimilar in one of the sexes. In most animals the female has the chromosome complex XX while the male has the unequal XY or merely a single X. In Lepidoptera, birds, and some fishes the opposite situation exists, the female being heterogametic. During meiosis there is a division of the pairs of sex chromosomes and autosomes, each gamete receiving the haploid number. In those organisms where the male is the heterogametic sex, half of the gametes of the male contain the

X chromosome, and half the Y chromosome. In the female all gametes are of the X type. At fertilization there is a restoration of the full complement. According to the laws of probability, if the meeting of the ovum with either one of the two types of spermatozoa is purely a matter of chance, half of the zygotes formed should be of the XX or female type and half of the XY or male type of sex chromosome complex. Barring the intervention of subsidiary factors which might override this simple mechanism, or influence the embryo during gestation, one would expect in a sufficiently large population that the ratio of males to females at birth would be 1:1. However, there are such complicating elements, some of them proven, others theoretical. These may be divided into three classes: (1) factors disturbing the normal mechanism of gametogenesis, (2) factors preventing the purely chance meeting of the ovum with either type of sperm, and (3) factors acting upon the embryo or foetus during gestation.

The first of these follows from the observation (Bridges, 1932; Witschi, 1934; and Goldschmidt, 1934) that the allosomes are not alone as the genetic determiners of sex, but that there are also sex factors located on the autosomes. The quantitative relationship between allosomes and autosomes determines whether the individual will possess a preponderance of factors for maleness or for femaleness. Bridges showed this relationship in *Drosophila melanogaster*. By a chromosome division without a separation into two nuclei, a tetraploid condition arises. Subsequent meiosis results in diploid eggs. When such eggs are fertilized by X sperms, triploid females result. The offspring from such triploid females may represent a variety of chromosome complexes and a wide range of sexuality

depending upon the ratio between the number of autosomes and the number of X-bearing chromosomes. The autosomes quite probably have an influence on sex determination in higher animals, and obtain varying degrees of expression through abnormal gametogenesis.

The second class of factors which may have a part in determining sex are only speculative. It will be shown presently that in all probability males and females are not conceived in equal numbers and several theories have been advanced to explain this apparent upset to chance fertilization. Sturtevant and Beadle (1939) suggested that although the two kinds of sperm are produced in equal numbers, the most likely reason for deviation from a 1:1 ratio of sexes at conception is a differential rate of motility between the X and Y types. Thus the eggs would be more frequently fertilized by the sperm with the greater rate of speed. Another possibility is differential selectivity and viability of the male-determining sperm. King (1918) selected rats for high and low sex ratios. She accounted for the difference in the two strains as being due to selective fertilization, the ova in the high ratio strain having a greater receptivity to male-producing sperm. These theories are discussed by Hartman (1939) who considers them unsusceptible of proof or disproof and likely to be perpetuated in the manner of folklore.

Studies on the sex ratio at birth have dealt almost exclusively with environmental factors which, acting upon the mother, produce a differential mortality between male and female embryos. These will be considered in detail in following sections. Whereas this is a process of selective elimination, a few other works indicate that determination or differentiation of sex may be influenced by factors acting subsequent to fertilization. Thus

Shull (1925), studying the rotifer *Hydatina senta*, the aphid *Macrosiphum solanifolii*, and the cladoceran *Simoccephalus vetulus* in their bisexual and parthenogenetic cycles, concluded that sex determination may depend partly upon differences in the metabolic level, but also upon other physical or chemical factors of the environment. In *Bonellia viridis* the chromosome mechanism, if present at all, must be very weak, for Baltzer (1937) found that extra-genetic conditions play the predominating rôle in sex determination of the larvae. If they become attached to the body of the adult female they develop into males, but separation from the body results in female development. This may be due to a secretion by the female or to other environmental influences such as differential acidity of the water.

Goldschmidt (1916, 1934) found that all of his studies based solely on sex chromosomes fell short of an adequate solution to the problem. Working with the gypsy moth *Lymantria dispar* he formulated a theory that sex is determined by a quantitative relationship between male and female sex-producing factors, M and F. In the heterogametic female *Lymantria*, F is inherited through the cytoplasm; in other forms in the autosomes. M is found always in the X chromosomes. The F and M factors differ in strength among different races of the gypsy moth, and certain combinations result in intersexes. The sex factors are supposed to produce substances which control the tissues of the undifferentiated organism so that either male or female is produced according to whichever substance is in excess. In the intersexes, the turning point from male to female, or vice-versa, depends on the rate of reaction of the two substances which, it is suggested, may be enzymes.

In his extensive work on *Rana temporaria*

Witschi (1929, 1934) concluded that, although sex in amphibians is determined by the quantitative relationship between genes of the sex chromosomes and autosomes, this mechanism is regularly eclipsed by environmental factors, resulting in sex races. The larval gonad possesses a cortex and medulla. During male development the cortex atrophies and the medulla becomes the inductor of sperm formation, while in female development the cortex becomes functional and induces formation of eggs. High temperatures prevent cortical growth, reversing the sex of female tadpoles by overriding the genetic factors. Low temperatures conversely inhibit medullary formation. Witschi (1934) did not believe that the morphogenetic substances belong strictly to the class of hormones in toads and frogs, but acted much like hormones in the newt. He based this conclusion on parabiotic twinning and gonad transplantations in *Triturus torosus*. King (1910) found that temperature may have an indirect action in the determination of sex in *Bufo*, but it was not the dominant factor.

Boring and Pearl (1918) described eight hermaphrodite fowl. These had embryonic or degenerating ovaries, and three of them were changing from a female to a male condition in behavior, secondary sex characteristics, and gonads. Such intersexes in birds have usually been attributed to sex hormones acting primarily during embryonic life, although the exact place of origin of such hormones has been contested. Moore (1925) believed this to be the case in the Leghorn chicken, and that a similar condition exists in mammals. Goldschmidt (1934) held that it is probable that vertebrates have embryonic hormones causing sex differentiation, although conclusive experimental data are lacking.

One of the most important studies on sex

hormones is that of Lillie (1916, 1917) on free-martin cattle. He brought forward embryological evidence that the heterosexual twins are dizygotic and the sterile free-martin is genetically a female. There is an anastomosis of the foetal circulations of the male and female embryos, so that the female organs of reproduction become degenerate due to the action of male sex hormones in the blood. The free-martin often develops some of the characteristics of the bull. Theoretically the reason that the reverse action never takes place is that formation of hormones in the male is more precocious than in the female.

Further evidence of the influence of hormones on sex differentiation may be implied by the well-known changes which occur in the body after castration or ovariectomy. Although such operations seem to result in the appearance of characteristics of the opposite sex, Marshall (1925) and Lipschütz (1924) declared that there is actually no evidence of a reversal, but rather an assumption of a neutral state. This neutral condition is more like the male than like the female among birds, so that avian castration results in only small changes, whereas ovariectomy appears to produce male characteristics.

Lipschütz formulated an hypothesis of sex determination based supposedly on the effect of hormones alone. According to this, the somatic constitution of mammals and birds is undifferentiated (bisexual or asexual) at the beginning of development. The condition is changed in a male or female direction during embryonic life by the differentiating sex gland and by this action only. This view follows from the observation that animals that have undergone castration or ovariectomy can be feminized or masculinized by transplantation of gonads of the sex opposite from the original. Lipschütz alleged further support from his observations on

intersexuality in man. He said "There is no need to assume special genetic factors for the male and female sex characters in mammals and birds. Transmission of the male sex characters by the female, and of female characters by the male can be explained on the assumption of a transmission of the characters of an asexual soma, which has the capacity to react in a male or female manner according to sex specific hormones, the latter being possibly not peculiar to the species." However, Lipschütz stated that the sex gland which produces such a hormone "is the morphological manifestation of the biochemical difference between a male and female fertilized egg." If one assumes that there is a biochemical difference, the question might be put as to what it is that originally determines whether a zygote is male or female. Examined under the light of genetic research, it seems certain that sex chromosomes are responsible for the determination of the zygote, and that the sex gland, which is in itself predetermined by the genes, gives rise to hormones that act as subsidiary factors of somatic differentiation.

Riddle (1927) pointed out that the metabolic requirements of the male are greater than those of the female, and suggested that this is a cause of the higher mortality of male embryos. The same view was expressed by Joyet-Lavergne (1929) in his earlier work on pigeons. Besides the possibility that the metabolic rate can effect the sex ratio at birth by a selective mortality, it has also been considered as an explanation of sex determination. Riddle (1932) advanced the theory that the X and Y chromosomes carry genes which influence oxidation. If the Y chromosome alone raises the oxidation rate in excess of a single X, then an XY complex will establish a higher rate than an XX combination. The XY gives rise to males and the

XX to females. There may also be genes in the autosomes which influence oxidation, but by and large they contribute equal effects, whereas the quantitative difference between X and Y results in unequal oxidation rates. The organism is capable of response to forced changes in oxidation at any time during its life. Consequently environmental or pathological conditions which disturb metabolism may account for sex-reversals. The case of a normal hen which became transformed into a functional rooster was explained by Crew (1923) as being due to a metabolic upset resulting from a tumor. Amar (1929) believed that carbohydrate feeding increased metabolism and caused a greater number of male births.

To summarize what is known about sex determination, it may be said that no single factor offers an adequate explanation, nor is the method constant throughout phylogeny. In some of the lowest forms the chromosome mechanism appears to be an unimportant factor and the question of sexuality is largely decided by the environment. Among insects, genetic elements obtain a high degree of control and sex results from the balance between genes of the autosomes and sex chromosomes. Intersexes arise from mutations or from chromosomal aberrations (Bridges, 1939). In the gypsy moth, however, the nuclear mechanism may be overridden by other sex factors, presumably enzymes or hormones. The situation becomes still more complicated among vertebrates. The sex chromosomes of amphibians can apparently be dominated by cortical or medullary secretions of the gonads, which in turn are subject to environmental influences. The degree of effect which environment may have in sex determination or differentiation among birds and mammals is largely unknown, but as Danforth (1939) says in his excellent review of the problem, "It

is doubtful if there are many forms, even among the higher vertebrates that are entirely free at all stages from susceptibility to environmental influences on their sexual differentiation." It has been postulated that the metabolic rate may influence sex determination by means of genetic factors, and there is some evidence that environmental conditions which alter metabolism may in certain cases result in sex-reversal. However, true sex-reversal is rare among higher vertebrates, and it is doubtful that metabolism has a significant rôle in either determination or differentiation of sex. It has been conclusively established that the embryo is somatically indifferent during the early stages (Willier, 1939), and that subsequent sex differentiation results from the action of male or female hormones. The endocrine organs producing these hormones are determined by the chromosomal mechanism, and there is a close interdependence of the two factors. Although hormonal or environmental influences can in some cases dominate the nuclear factors during differentiation, it appears that determination of sex is primarily a genetic process taking place at the time of fertilization.

THE SEX RATIO

Why vital statistics "should be made known to the People, otherwise than to please them, as with a curiosity, I see not. Nor could I ever yet learn (from the many I have asked, and those not of the least Sagacity) to what purpose the distinction between *Males* and *Females* is inserted, or at all taken notice of?" John Graunt, who wrote this passage concerning the Bills of Mortality, nevertheless presented in 1676 the first observations known on the proportion of sexes in a large population. He found that from 1628 to 1662 there were christened in London 139,782 males and 130,866 females, the country

accounts also showing an excess of males. In London the proportion was 13 females for 14 males; in Hantsire (a country parish), 15 for 16; and in Cranbrook, 19 for 20. Graunt commented upon the greater proportion of male births in the city than in the country, and recommended the variation to the examination of the curious. He further observed that more males than females died of violent deaths, drownings at sea, war, and at the hands of justice, and more went unmarried to the colonies. Yet, because of the excess of male births, each woman might still have a husband. This he considered a blessing to mankind, being a natural bar to polygamy, for in polygamous unions a man must dominate his wives, financially and otherwise, to keep them at peace with each other and in awe of himself, "the poorest Subjects being the most easily governed." As to the male excess, "What the Causes hereof are, we shall not trouble our selves to conjecture, as in other Cases: only we shall desire, that Travellers would enquire, whether it be the same in other Countries."

It appears that Captain Graunt's own curiosity overwhelmed his initial pessimism. His recommendation has been taken seriously, and later students have found that the excess of males in human populations extends throughout the world. Moreover, in large groups and under general conditions, the proportions of the sexes are fairly constant. This is true also of other animals, although inter-specific differences exist in the sex ratio, there being for some forms an excess of males, for others an excess of females. Such constancy within the species indicates a deep-seated mechanism of sex determination, such as the chromosome mechanism described in the previous section. However, it was also noticed that the genetic factors themselves may be modi-

fied, and that there are subsidiary factors which are capable, in some cases, of dominating the nuclear control of sex. One would thus expect intraspecific variations in the sex ratio at conception (or at the time of embryonic differentiation). This is referred to as the primary sex ratio. Variations in the proportions of sexes at birth, or the secondary sex ratio, are dependent not only upon the primary ratio, which results from the sex-determining mechanism, but also upon the sex-differential rate of prenatal mortality, a potential sex-selective mechanism. What are the specific conditions which may influence the sex-determining or sex-selective factors, and give rise to variations about the norm for the sex ratio in a particular species? Volumes of literature have been written in an attempt to answer this question.

Inheritance of the sex ratio

Whether or not sex ratios are inheritable is a topic of considerable controversy. Parkes (1926a) stated that the issue becomes a question of what factors resulting in a variation of the sex ratio could be of an inheritable nature. A large body of evidence has been accumulated to show that abnormally high or low ratios in *Drosophila* may be transmitted through successive generations. Rawls (1913) described flies which produced approximately two females to each male. The method of transmission in this case was shown by Morgan (1912) to be a sex-linked lethal factor on the X chromosome. The recessive lethal was always dominated in the female by the normal allele, but half of the sons received the fatal X and died before emergence. Sturtevant (Morgan, Bridges, and Sturtevant, 1925) described a mutation in *Drosophila affinis* which resulted in the production of very few males, and Gershenson (1928) reported a similar

case in *Drosophila obscura*. In the latter study 96 percent of the flies were females. Examination showed the causal factor to be a sex-linked gene which acted previous to fertilization. Apparently it caused almost total removal of the Y-type of spermatozoa, behaving much like a gametic lethal. The presence of an inheritable character producing an excess of males in the ratio 5.5:1 was shown by Redfield (1926). She believed that the lethal took effect during the egg stage, probably within the mother's body. Bridges (1917), Mohr (1923), Bonnier (1923), and Mohr and Sturtevant (1919) gave data on other lethals which caused transmissible variations in the sex ratios of *Drosophila*.

Woods (1906), writing shortly after the discovery of sex chromosomes, concluded that sex determination was not according to Mendelian principles, nor was the sex ratio inherited. Using genealogies of the reigning houses of Europe, he made a four-fold correlation table of parental and filial fraternities which showed either an excess of males or an excess of females. The correlation was positive, but statistically insignificant. A similar investigation was conducted by Heron (1906), although he correlated sex ratios of individual sibships in two successive generations. The four correlations made for man were, as in Woods's study, positive but statistically insignificant. Stud book entries were likewise subjected to this treatment with the same results. Heron stated that inasmuch as this material showed no sensible inheritance of sex, variations in the ratio are not racial, but must be associated with environmental factors. Pearson analyzed Weldon's (1906) data on Japanese waltzing and albino mice. He made correlations of filial sex ratios with parental and grand-parental ratios, finding positive correlations in the first case, and negative in the second, all low and insignificant. This

agreed essentially with the findings of Woods and Heron.

These three studies are subject to the same criticism. The multiplicity of factors which may influence sex determination or sex ratio was at that time unrecognized, and no account was taken of such factors. With unselected matings in a general population a high correlation of sex ratios between generations could hardly be expected. The authors failed to take cognizance of the fact that the sex ratio *per se* may not be inherited according to Mendelian laws, but that, as previously mentioned, there is a question of what inheritable factors may give rise to sex ratio variations. An investigation by Willoughby (1931) showed a probable tendency toward inheritance of the sex ratio. The correlation between the sex ratios in fraternities of the individuals considered and the sex ratios of paternal and maternal cousins were particularly high, being $.52 \pm .06$ and $.68 \pm .04$ respectively.

Moenkhaus (1911) selected *Drosophila ampelophila* for high and low sex ratio strains. He found a normal ratio of 1 male to 1.126 females in 26,933 flies. Starting with two pairs from nature he selected for six generations. The high male strain remained only slightly above the norm during each generation. The strain high in females continued high, however, being as great as 1 male to 2.17 females in a particular generation. Another generation threw 1 male to only 1.36 females, and Moenkhaus explained this as an unfortunate selection of parents. The conclusion was drawn that sex ratio is a quality that is "strongly transmissible and amenable to the process of selection," the female being almost entirely responsible. Warren (1918), in criticizing this experiment, alleged that a low ratio in a particular generation could not be due to a poor selec-

tion of parents, since selection has a cumulative effect. The criticism seems not well grounded when one considers how few generations the experiments covered. There may easily have been a pair of flies which would throw an unfavorable ratio. Warren believed that the maintenance of a high proportion of females was due to a sex-linked lethal in the female strain, although there is now no way by which this can be conclusively demonstrated. Warren's own selection experiment with the same species showed only slightly divergent ratios, by which he concluded that selection cannot alter the proportions of sexes.

A much more extensive selection experiment was conducted by King (1918) on albino rats. The mean ratio of out-bred rats was found to be 104.6 males per 100 females. Animals were inbred for six generations before selection began, and the sex ratio differed by an insignificant amount from the established norm and from a control group. This agreed with Moenkhaus's (1911) observation on inbreeding in *Drosophila*. Having established that inbreeding in itself had no correlation with masculinity, King started selection in the seventh generation from a single pair mating. Her results are summarized in Table 1.

Rats from each series were later bred to stock animals and showed the tendency of the particular series, but to a lesser degree. Moreover, the female seemed to exert the greater influence on determination of the ratio. King agreed with Moenkhaus that sex ratio is probably an inherent characteristic and amenable to selection.

Although the *Drosophila* studies were based on too few generations and insufficient numbers to warrant any conclusion as to the effect of selection, the albino rat experiment largely overcomes objections.

Tentatively, at least, the interpretations seem justified.

Darwin (1874) considered this problem in *The Descent of Man and Selection in Relation to Sex*. The method of selection to which he had recourse was the practice of female infanticide among certain populations. The reasoning was that families having an excess of females destroyed a greater proportion of the children than families having an excess of males. If sex ratio is a transmissible character, then the bias in favor of a male-producing race should increase with successive genera-

TABLE 1

Showing, by generation groups, the sex ratios in the inbred litters of male and female lines

(Adapted from King, 1918)

GENERATION	SERIES A (HIGH STRAIN)		SERIES B (LOW STRAIN)	
	No.	Sex ratio	No.	Sex ratio
1-7	930	110.4	932	109.0
8-10	779	112.5	795	92.5
11-13	953	130.7	876	84.0
14-16	999	126.5	888	76.9
17-19	1144	121.7	1083	77.3
20-22	1270	122.0	1102	84.6
23-25	1129	123.5	1149	78.7
8-25	6274	122.3	5893	81.8

tions. Darwin found on good authority that female infanticide which had been long practiced in New Zealand, was almost extinct by 1835 and entirely so by 1844. In a limited area where the population was carefully studied, the "non-adult" males numbered 178 and the "non-adult" females 142, a sex ratio of 125.3 to 100. These figures are for the year 1858. If "non-adult" meant children under 14 years of age, the ratio may indicate a selection, especially inasmuch as there is a higher male than female mortality during infancy and childhood. However, the numbers are meagre, and if

the "non-adult" category included individuals over 14 years of age, the proportions are possibly distorted by the infanticide. Certainly the adult figures which Darwin gives for New Zealand are of no significance in the problem. In the Sandwich Islands infanticide had ceased by 1819. In 1839 the males under fourteen years in Kauari and under 18 in Oahu numbered 1797, while females of corresponding ages numbered 1429, giving a sex ratio of 125.75. A census of all the islands in 1850 gave the number of males and females under 17 years of age as 10,733 and 9,593 respectively; a ratio of 112.3 to 100. In 1872 the adult population had a ratio of 125.36 males to 100 females. Darwin was of the opinion that due to differential rates of mortality, the ratios would have been even higher had they referred to births. He concluded that there is reason to believe that selection of this sort tends to make a male-producing race, but did not believe that a similar process occurring in nature accounted for the deviation from a 1 to 1 ratio in a general population for either man or other animals.

Although the information is meagre concerning inheritance of the sex ratio, the weight of the evidence indicates that lethal factors and probably unknown others of an inheritable nature give rise to transmissible variations from the normal sex ratio of the particular species.

Hybridization

Several studies have indicated that hybridization increases the proportion of male offspring. King (1911b) mated albino rats with wild Norway rats and found a sex ratio of 119.07 among 425 births. The ratio used as normal for the albinos in the experiment was 106.46. King assumed that *Mus norvegicus* had approximately this same proportion of sexes, although a later study (King, 1924)

demonstrated that the wild rat has a much lower ratio. A high proportion of males was also found in hybrids of the deer-mouse, *Peromyscus*, by Sumner, McDaniel, and Huestis (1922). In 1930 offspring of pure matings they found 93.27 males per 100 females, whereas the hybrids had a ratio of 104.76 per 100. The difference divided by its probable error gave a critical figure slightly less than 3. It was suggested that the high hybrid ratio might have been due to a selection of male-producing spermatozoa by the ova, or that greater vigor resulting from cross-breeding may have influenced the metabolic rate. Theoretically this would have a differential effect upon male and female foetuses. The view is of course purely speculative. Guyer (1909) also thought that metabolism might be the determining factor in producing the higher sex ratio of hybrids. Hypothetically, the incompatibilities between two dissimilar germ plasms would result in a lowering of the metabolism of the embryo. This, Guyer believed, would be hostile to female development. However, in view of the greater metabolic requirements of the male, it would seem at least equally plausible that decreased metabolism might be inimical to male development. The original proposition is probably false. Guyer's study of museum specimens included 51 hybrid birds of known sex. Of these, 33 were pheasant crosses, among which there were but 4 females. The remainder, Guinea fowl $\times$ chicken and pheasant $\times$ chicken, were all males. This very abnormal distribution of sexes may have resulted from a selection of male specimens for museum pieces. Moreover, as the author realized, there is no indication of the probable ratio at the time of hatching. Riddle (1925) reported no females in 61 offspring of common pigeon $\times$ ring dove crosses. A highly specialized case wherein selective elimina-

tion of foetuses affects the sex ratios of hybrid births, is that of the bison and cattle crosses described by Babcock and Clausen (1918). The pelvic dimensions of the domestic cow are unsuited to the shape of the male hybrid foetus. Consequently the males seldom reach full term, and live births are predominantly female.

Pearl and Pearl (1908) studied the ratios of cross matings as computed from vital statistics of Buenos Aires, 1896 to 1905. They found that the Italian $\times$ Argentine ratio of $105.72 \pm .46$ and the Spanish $\times$ Argentine ratio of $106.69 \pm .74$ were, except for one comparison, significantly higher than the proportions of sexes among pure matings of these groups. The single insignificant difference was in the same direction as the others, and as the authors stated, does not invalidate the general result. The Buenos Aires data are particularly valuable for such a study since the pure Argentines are, in a genetic sense, strictly homozygous. This study considered the possibility that the greater excess of males in the cross matings was due to a difference in the proportion of stillbirths, age of parents, or environmental conditions. The conclusion was reached that these factors probably played an unimportant part, if any, in determining the observed variations. Lewis and Lewis (1906) also concluded that cross matings in the Buenos Aires population produced high sex ratios. Studies by Little (1919, 1920) of hospital births in New York City supported the earlier investigations. This author found a ratio of 106.27 in 5,753 progeny of pure matings, while that of 1,303 hybrids was 121.56. The difference was 6.76 times its probable error. These figures included stillbirths and abortions, the percentages being 6.17 in pure matings and 3.98 in crosses. Little explained the lesser amount of reproductive wastage in cross matings as being

characteristic of greater vigor among hybrids. He alleged that there was less chance for duplication of adverse recessives in zygotes resulting from different stocks.

A study by de Jastrzebski (1919) failed to support the view that hybridization increases the proportion of males. In this work the sex ratio of offspring from mixed parentage was midway between that of pure native and pure foreign for Uruguay, lower than pure matings for the United States in 1915, and higher than pure matings for New York City. The inconsistency of the results led de Jastrzebski to conjecture that the sex ratio of hybrids depends on the nature of the cross. It must, however, be recognized that the registration of vital statistics in Uruguay has not been, in the past, adequate for any critical investigation, much less when these statistics are broken down into nationality groups. When we couple with this fact the knowledge that a "pure" mating in the United States is practically non-existent, it is obvious that de Jastrzebski's conclusions are unfounded. An investigation by Russell (1936) failed to show any consistent elevation of the sex ratio due to cross-breeding of immigrants in the United States. Ciocco (1938a) also analyzed the masculinity of hybrid births in the United States from 1917 to 1934. He made sex ratio comparisons of foreign $\times$ native white with pure foreign and pure native white for five nationalities. Of twenty such comparisons the hybrid sex ratio was higher than that of either of the pure matings in 5 cases, intermediate between them in 9 cases, and lower in 6 cases. This investigation suggested that cross mating does not always result in an increased proportion of males. Ciocco concluded that the hybrid ratio possibly was a resultant of the relative levels of the sex ratios of the nationalities of the parents. But his

studies on this point lack any great critical significance because of the fact that his "pure native white" groups are anything but "pure" biologically in the genetic sense. Statistically all United States white populations are more heterozygous than even any European population and much more so than any truly "native" population, in the sense of a primitive indigenous population. This applies equally to the United States data utilized by Russell.

A substantial body of data indicates that hybridization increases the masculinity of births in man as well as in lower animals. Studies which contradict this are found, upon close examination, to be based upon figures unsatisfactory for this type of study. It is quite probable that the greater biological vigor which accompanies hybridization is in some way responsible for the results observed.

STILLBIRTHS AND ABORTIONS

Darwin recognized as a weakness in his study the fact that in dealing with a primitive people the sex ratio might be higher because of greater ease in parturition and consequently fewer stillbirths. It is almost universally accepted among biologists that stillbirths and also abortions are more frequent among males than among females. The literature refers almost exclusively to human material. However, King (1921) found the sex ratio of 415 stillborn albino rats to be 129.3 males per 100 females whereas the liveborn ratio of 31,670 individuals was 104.1. Among cattle, Johannson (1932) reported that 57.33 percent of all stillbirths and 58.86 percent of all abortions were males. Goehlert (1882) showed that in horses 135,826 living foals were in the ratio 96.57 males to 100 females, while stillbirths showed 106 to 107 males for each 100 of the opposite sex. For man, Bertillon (1875)

reported 134.1 as the sex ratio of stillbirths in Belgium during the years 1851-1860. Auerbach (1912) placed the figure for Budapest as 123.6. Wolda (1927) gave 117 to 133 as the range of sex ratios among stillbirths in Holland during the years 1901 to 1910. The average for Canada, 1925 to 1930, was given by Wyllie (1933) as 132 males per 100 females. Heape (1908a) put the stillborn sex ratio of Cuba at 144.45. For the United States, Ciocco (1938a, 1938b) gave the mean proportion of 68,932 stillbirths during the ninth month of uterogestation as 1346.9 males

TABLE 2

The sex ratio of abortions according to the duration of pregnancy

MO:	SEX RATIO OF ABORTIONS				
	Ciocco (1938b)	Greulich (1931)	Schultz (1921)	Auerbach (1912)	Bertillon (1893)
1	228.00	357.48	—	—	180.0
2	431.13		—	452	
3	361.00		121.0	322	
4	201.22	223.14	117.5	229	118.5
5	139.61	139.36	109.6	163	
6	122.74	128.91	87.5	116	112.1
7	112.40	116.60	108.5	116	116.4
8	124.75	125.26	133.3	—	108.7
9	134.69	137.43	167.6	—	131.7
10 and over	133.28	150.13		—	—

per 1000 females in the years 1925 to 1934. The sex ratios of abortions according to the period of uterogestation are given in Table 2.

The sex of embryos aborted during the early months of gestation is difficult to determine from a superficial examination. In Ciocco's material the sex of abortions during the third month was recognized in 63.2 percent of the cases, during the second month in 27.8 percent, and during the first month in only 10.1 percent. These data and those of Greulich, Auerbach, and Bertillon were obtained from official statis-

tics. The figures given by Schultz, although based upon fewer cases (1,410), resulted from careful examination of each foetus. Consequently the ratios which he gave during the third and fourth months may more closely approximate the true proportions than do the others. Auerbach's figures for these months were estimations and are probably excessive.

Material such as the above has been taken along with citations as to the total incidence of abortions at various periods of uterogestation, and from these figures estimations have been made of the sex ratio at the time of conception. Assuming a live born proportion of 105.5 males to 100 females, Schultz (1921) computed the primary sex ratio as 108.74. This differed but little from his earlier (1918) estimation of 108.47. Auerbach placed the figure at 116.4, while the ratio based on Ciocco's data is 137.22. Such wide variations are to be expected in view of the unreliability of the material upon which these ratios are founded. Nevertheless, they are an indication of the amount of deviation from the simple 1 to 1 ratio that would be expected from chance fertilization of ova by either X- or Y-bearing spermatozoa, if these exist in equal numbers. Boldrini (1936) dissented from the idea that the sexes are conceived in unequal numbers. It was his conviction that many abortuses at all stages, and particularly during the early months of gestation, are described as males when they are actually females. The excess of males at birth, according to Boldrini, is due to a higher rate of prenatal mortality among females. The data from which he drew his conclusions are far from convincing, and the results are incongruent with all other observations.

Considerable controversy has existed as to the reason for the higher incidence of mortality among male embryos and fo-

tuses. Holmes (1926) believed that the male is inherently weaker than the female, constitutional differences between the sexes being the discriminating factor. Wyllie (1933) and Auerbach (1912) also considered the male to possess an inferior vitality. King (1921) advanced the hypothesis that the difference in constitutional vigor between male and female has its foundation in a difference in the chromatin structure of the two types of zygote. It has been postulated that sex-linked recessive genes are responsible, and Holmes believed this to be a real though minor factor. An anonymous (1937) writer was also a proponent of the theory of sex-linked semi-lethals among those organisms where the female is the homogametic sex. The lower viability of males in species where the female is heterogametic was accounted for by the greater metabolic requirements of the male organism. Riddle (1927) revolted at the thought that the male is inherently the weaker sex. The mere fact that more males die during gestation does not prove that they are genetically inferior unless it is shown that male and female embryos are subject to identical conditions in utero. Since the male has greater metabolic and nutritional needs, this can, according to Riddle, serve as a prenatal death selector for sex. Furthermore, filterable female sex hormones of the mother probably have an adverse effect upon the male embryo. Most other writers who have disagreed with the view that the male is inherently weaker, have believed that the difference in sex incidence of prenatal mortality is due to the larger size of the male foetus. Greulich (1931) attributed the rise in the sex ratio of abortions after the seventh month to this cause. Data from the Clinique Baudelocque presented by Pinard and Magnan (1913a, 1913b) showed the numbers of deaths during gestation to be 618 males and 611

females; during labor, 467 males and 351 females; and within 11 days after birth, 867 males and 614 females. These writers concluded in opposition to other studies that there is no difference in sex mortality during pregnancy. They attributed the difference during and shortly after labor to an excess of obstetrical traumatism among males as a result of their greater weight. It is quite conceivable that the larger size and greater metabolic requirements of the male may be selective for death in the last few months of pregnancy, but it is difficult to believe that the maternal organism is incapable of responding to the slight difference early in gestation.

Ciocco (1938b) classified prenatal mortality and sex ratio according to the causes of death, and in relation to the duration of uterogestation. It is to be expected that the size of the foetus would have the greatest effect upon mortality caused by difficult labor. Ciocco's figures for this category are as follows:

GESTATION PERIOD	TOTAL	8 MOS. AND OVER	5-7 MOS.	4 MOS. AND UNDER
Percent of males	62.7	62.9	55.9	70.0
Percent of prenatal mortality	100.0	96.9	3.0	0.1

Little significance can be attached to the sex ratio for four months and under as it must be based on very few cases (probably 16 since the total number of stillbirths due to difficult labor amounted to 15,755). Furthermore, the sex and cause of death of such young embryos are difficult to determine with reliability. Of all the causes of death, the sex ratio 62.9 is the highest for the group 8 months and over, while 55.9 is one of the lowest in its period. Thus it would appear that foetal size affects the sex ratio of stillbirths predominantly during the final months of pregnancy. In regard to the total sex

incidence of abortion, Ciocco found the masculinity to be lowest in cases of defective embryonic development (malformations) and high as a result of faulty or diseased placental structures. The highest ratios were associated with malpresentation and difficult labor. Ciocco stated:

One of the most important correlaries to be drawn from these observations is that apparently there is no evidence to justify the current assumption that the males under all conditions are more liable to stillbirth. Consequently the theories which seek to explain the so-called masculine inferiority on the basis of chromosome structure, metabolism, vitamin requirements, etc., need to be modified considerably in order to be consistent with the above findings.

It is probable that all of the factors considered have some part in the differential elimination of foetuses of the two sexes, but the difference cannot be attributed exclusively to any one of them. The data are not only inconclusive concerning the later months of pregnancy, but the greatest handicap lies in the void of knowledge existing in the early periods when, apparently, the masculinity of abortions is at a maximum.

By far the most widely accepted explanation for variations in the sex ratio at birth is that of differential rates of prenatal mortality. Since the sex incidence of abortions and stillbirths is greater among males, a group which has a low intra-uterine death rate will demonstrate a higher sex ratio among living offspring than a group which has a high proportion of prenatal deaths. It will be noted that such an assertion, if put forward as the sole cause for variations in the ratios of sexes at birth, requires proof that the primary sex ratios and also the sex incidences of antenatal mortality of the groups under consideration are equal, or differ in an amount or direction which can have no significant part in determination of the observed variations. Because such a proof

is very nearly impossible, it is not surprising that it has been overlooked or taken as a postulate, largely because variations in prenatal mortality rates are such a ready explanation of differences in secondary sex ratios. If reproductive wastage is the sole factor, any increase in the rate of stillbirth and abortion should be accompanied by a decrease in the proportion of males among live births. A small amount of data by Parkes (1924a) on mice suggested that this might be true. MacDowell and Lord (1925) made a similar study of mice on a much larger scale, and found no relationship. Ciocco (1938a) investigated the problem in man by calculating the co-variation between changes in the prenatal mortality rate and the live birth sex ratio for successive years in selected areas of the United States. He found that in 50.8 percent of 236 possible changes, both the incidence of prenatal mortality and the secondary sex ratio increased or decreased together, while in 49.2 percent they changed in opposite directions. There was no statistically significant difference from the expected 50 ± 3.3 percent. Similar insignificant differences were obtained in co-variations between the sex ratios of live births and of stillbirths and abortions. Although the amount of prenatal mortality in some cases has an important part in determining variations of the secondary sex ratio, it certainly cannot be the only cause. In view of the rigorous requirements of a proof that it is the sole cause, dogmatism on this point would seem a poor policy. Nevertheless, a number of writers have alleged that such is the reason for differences which they observed in secondary ratios, without giving consideration to other possible factors.

VARIATION IN THE SEX RATIO AT BIRTH

Supposedly normal sex ratios of various animals are presented in Table 3, along

with reference to the source. These ratios are confined to dioecious and non-parthenogenic forms and of necessity largely concern laboratory and domesticated animals. Information is so meager on sex ratios of forms lower than birds (except for a few insects and amphibians) that it is doubtful if these data can be considered as representative even for the species, to say nothing of the general phylogenetic level. The most widely studied of the insects, *Drosophila*, under normal conditions has a surplus of females at emergence. The sex of amphibians is usually determined in only a fraction of the total offspring, and the ratio varies according to the period of life at which they are sexed and with environmental conditions (Witschi, 1934; King, 1909). Sex reversal and hermaphroditism are common in amphibians, and there is wide geographical variation in the proportions of the sexes. The problems involved cannot be discussed in the present paper, and a mere listing of the sex ratios would be meaningless. The sex ratio of the domestic fowl has been studied with sufficient care to warrant the conclusion that the proportion of females is always greater than that of the males. Heape's (1907) figures on the canary were obtained from two breeders. It is doubtful if these are of any great value inasmuch as the numbers are not only small, but the parent birds were kept under widely diverse conditions. The difficulties of obtaining correct sex ratios for wild birds were overcome by McIlhenny (1940) in his study of the Gulf Coast Redwing and Boat-tailed grackle. These birds are both of the family Icteridae, both lay three eggs to the brood, and the sex can in each case be determined in the nestlings. In those nests which contained a full complement of offspring the redwing had a male percentage of 76.9 while that of the grackle was 30.3. The male percentage of the trapped and banded birds of these same

TABLE 3
Sex ratios among lower animals

Canary.....	68	353.3	Heape (1907)
Gulf Coast Redwing.....	420	332.9*	McIlhenny (1940)
Dog, German Shepherd.....	1,400	124.3	Whitney (1939)
Lepidoptera, <i>Bombyx</i> (several species).....	1,695	122.7	Darwin (1874)
Fig.....	2,357	111.8	Wilckens (1886)
Mouse, albino.....	2,903	111.0	Parkes (1926b)
Dog, greyhound.....	6,878	110.1	Darwin (1874)
Rat, albino.....	1,001	108.0	Slonaker and Card (1923)
Cattle.....	4,900	107.3	Wilckens (1886)
Guinea pig.....	7,989	106.92	Ibsen (1922)
Cattle.....	124,166	106.3*	Johansson (1923)
Rat, piebald.....	2,845	106.0	King (1924)
Pigeon.....	1,648	105.23	Cole and Kirkpatrick (1915)
Rat, albino.....	2,818	104.6	King (1918)
Rat, albino.....	31,670	104.1	King (1921)
Mouse, albino.....	2,322	103.1*	MacDowell and Lord (1926)
Coleoptera, <i>Tribolium confusum</i>	2,500	102.8*	Schneider (1940)
Fig.....	5,380	102.6	Parker (1914)
Mouse, Japanese waltzing and albino.....	479	102.0*	Weldon (1906)
Cattle.....	1,313	100.2	Pearl (1917a)
Fish, <i>Gambusia</i>	2,593	100.2	Hildebrand (1927)
Horse.....	25,560	99.7	Darwin (1874)
Sheep, Cheviot and black-faced.....	50,685	97.9	Darwin (1874)
Guinea pig.....	2,014	97.8*	Schott and Lambert (1930)
Diptera, <i>Drosophila melanogaster</i>	31,097	97.8	Lawrence (1940)
Diptera, <i>Drosophila ampelophila (melanogaster)</i>	15,002	97.7	Hyde (1914)
Sheep.....	6,751	97.4	Wilckens (1886)
Mouse, <i>Peromyscus</i>	5,050	97.37	Sumner, McDaniel, and Huestis (1922)
Horse.....	16,091	97.3	Wilckens (1886)
Sheep, Leicester (one year old).....	8,965	96.7	Darwin (1874)
Horse.....	135,826	96.57	Goehlert (1882)
Pig, Duroc-Jersey.....	16,233	95.4	Parkes (1923)
Mouse, albino.....	3,308	95.2*	Crew (1925)
Diptera, <i>Drosophila ampelophila (melanogaster)</i>	35,000	95.0	Warren (1918)
Domestic fowl.....	1,001	94.7	Darwin (1874)
Cattle.....	982	94.4	Darwin (1874)
Domestic fowl.....	20,037	94.4	Pearl (1917b)
Domestic fowl.....	2,396	93.8*	Jull (1924)
Domestic fowl.....	2,501	88.0*	Lambert and Curtis (1929)
Rat, wild Norway.....	1,862	85.8	King (1924)
Fish, <i>Coregonus albus</i> (adults).....	841	84.8	Pearl (1916)
Mouse, albino.....	1,469	79.8*	Bluhm (1924)
Canary.....	200	76.99	Heape (1907)
Boat-tailed grackle.....	412	43.5*	McIlhenny (1940)
Siphonaptera, several genera (adults).....	—	40-60	Shaftsbury (1934)
Terrapin (adults).....	1,433	16.2	Hildebrand (1933)

* Computed from male percentage.

species was found to be a few points higher. Mayr (1939) in his study on the sex ratio of wild birds, considered such species variations to be a result of accessory genetic factors which modify the sex-determining mechanisms.

The several investigations on mice show a considerable amount of variation even in the albino strain. This differs from the situation found for rats in the excellent studies of King. The wild Norway was the only strain which had an excess of females. The dog has, in all studies, demonstrated the highest male sex ratio of any of the mammals. Among the ungulates the masculinities reported for the horse are low and quite constant, falling between 96 and 100. Gini (1908), in his extensive table on this animal, cited only one example wherein the number of males exceeded the number of females. Sheep likewise produce an excess of females, whereas cattle and pigs may vary in either direction from an equality of the sexes.

Data on sex ratios found in man are presented in Table 4.

These figures supposedly represent the condition found in a general population of each country under consideration. The table takes no account of secular variations. In all cases there is a higher proportion of male births than of female births. The ratio is seldom less than 104 or greater than 107 and is generally considered to average about 105.5 males per 100 females or 51.34 percent. Oppenheim (1926) reported a masculinity of 107.8 in 6698 Chinese births. Russell (1936) found the lowest sex ratios in Salvador and Japan, and the highest in Greece and Korea. The most comprehensive list of sex ratios for various countries was compiled by Gini (1908). Many of his figures were of early date and probably inaccurate due to faulty registration. Only a few of the ratios reported by him are given in

Table 4, and these are taken from the period 1896 to 1900. The highest masculinities which he reported were for Greece, Rumania, and Spain, which are approximately 111. No very low ratios were reported, the remainder falling generally

TABLE 4
Sex ratios in man

DESCRIPTION	MALES PER 100 FE- MALES	AUTHORITY
Greece.....	113.2	Russell (1936)
Korea.....	113.1	Russell (1936)
Spain.....	111.1	Gini (1908)
Austrian Jews.....	109.1	de Jastrzebski (1919)
Cuba (whites).....	108.4	Heape (1908a)
Bulgaria.....	108.3	Gini (1908)
Austria.....	106.5	Gini (1908)
Italy.....	106.5	Gini (1908)
Norway.....	106.4	Gini (1908)
Sweden.....	106.2	Gini (1908)
France.....	106.2	Darwin (1874)
United States (native whites).....	106.2	Ciocco (1938a)
Finland.....	106.0	Gini (1908)
Germany.....	106.0	Gini (1908)
Holland.....	106.0	Gini (1908)
Denmark.....	105.7	Gini (1908)
France.....	105.5	Gini (1908)
Italy.....	105.5	Savorgnan (1933)
Cape Colony (whites).....	105.4	de Jastrzebski (1919)
Japan.....	104.6	de Jastrzebski (1919)
England.....	104.5	Darwin (1874)
England and Wales...	104.3	Russell (1936)
Japan.....	104.3	Russell (1936)
United States (colored).....	102.8	Ciocco (1938a)
Cape Colony (blacks).....	102.6	de Jastrzebski (1919)
Cuba (colored).....	101.1	Heape (1908a)

between 105 and 106.5. Gini stated that France demonstrated a low ratio in the years just preceding his publication, and this is born out by figures of Lewis and Lewis (1906) and of de Jastrzebski (1919). The former authors likewise found high

ratios for Greece, Rumania, and Spain. The custom of presenting sex ratios by nationalities was criticized by de Jastrzebski, since these groups are not composed of racially homogeneous populations. Accordingly he divided Austria into several provinces, the people of which he claimed were relatively pure racially, although living under comparable conditions. These groups showed a variation in masculinity from 103.7 for the Serbo-Croats to 106.5 for the Italians. A similar division of India resulted in marked sex ratio differences for the several races.

All investigations on a sufficiently large number of cases show a lower masculinity of black races than of white. Gini pointed this out for Africa and for Queensland, while Heape's figures showed a wide variation between blacks and whites in Cuba. The low sex ratio of Negroes in these same countries and in parts of the United States was also demonstrated by de Jastrzebski. Although nearly every writer considered the differences to be a manifestation of racial characteristics, Huntington (1938) believed that they probably result indirectly from environmental factors. However, the weight of the evidence indicates that there are variations with race or nationality in man just as there are variations with species in lower animals.

SOCIO-ECONOMIC VARIATIONS

Students of sex ratio problems have generally alleged that socio-economic variations are due to differences in the amount of prenatal mortality. This view was taken by Winston (1932) who analyzed data on 5,466 families from *The Abridged Compendium of American Genealogy*. In a socially select group of 15,763 children, he found a sex ratio of 112.0. This high ratio was attributed to greater care and training of mothers with a consequent

reduction of stillbirths. From United States governmental data the writer cited a stillborn sex ratio of 150.7 for 341 cases where the foetal death resulted from adverse economic conditions, namely, overwork of the mother. This stillborn ratio, it will be noted, is much higher than any of those previously mentioned. Crew (1937) stated that the sex ratio "is affected by social status, being higher in the upper and middle classes and lower amongst unskilled workers." He minimized the possibility that this resulted from any other cause than differences in prenatal mortality, and postulated that changes in the sex ratio at birth could be used as an index of the efficacy of public health measures such as slum clearance and social service. Punnett (1904), who studied the sex ratio in poor and wealthy classes in London concluded that a low masculinity was associated with low social status. Russell (1936) upheld this conclusion in his analysis of social classes in England for the year 1921.

The results of Lewis and Lewis (1906) conflict with the above studies. Among 2,877 Scotch professional families these authors found a sex ratio of 1032 males per 1000 females. In the working class the ratio was 1037 for 49,427 births. Offspring of commercial, agricultural and seafaring classes had sex ratios between 1066 and 1070. It must not be overlooked that the Lewises were severely criticized at the time of the appearance of their memoirs because all the Scottish data upon which their conclusions mainly rested were for live births only and took no account of stillbirths or earlier intra-uterine mortality. Kisch (1887) and Wall (1887) examined masculinity rates among European royalty, and found ratios of 107.7 and 107.4 respectively. Caution must always be exercised in interpreting sex ratios from royal genealogies, since there

may have been a tendency to underemphasize female births. Wall stated that masculinities were high among the peers in England, and also among the lowest classes whereas the middle classes contributed more to the female births. He alleged that these variations were due to differences in the age of the parents, a viewpoint shared by Russell. This subject of age of parents will be discussed in a later section.

The question of variation in sex ratio according to urbanity is a corollary to that of social and economic differences. John Graunt called attention to a greater proportion of male christenings in London than in the country. The urban ratio based on his data is 107.19 while that of a rural district is 105.61. The accuracy of the records at that time (1569-1664) is of course questionable. Dusing (1891), who investigated this problem in Prussia, found the reverse situation. His figures showed an almost linear increase in masculinity with decreasing urbanization. Lewis and Lewis (1906) demonstrated the same trend for births in Scotland. Omitting illegitimate births, the sex ratio was for principal towns 104.9, large towns 105.2, small towns 105.4, mainland rural districts 105.5, and insular rural districts 107.0. These authors did not consider the possible influence of prenatal mortality, but concluded that the factor of legitimacy had no part in determining the observed differences. Urban and rural sex ratios for a number of other countries were also given by Lewis and Lewis and this list was extended by de Jastrzebski (1919). Each of the ten countries studied showed a higher ratio in the rural populations than in the urban.

Vigor and Yule (1906) found no such clear-cut distinction in masculinity according to the degree of urbanization in England and Wales. Their data showed a

high proportion of males in semi-urban populations and a lower proportion in large cities and in purely rural groups. Ciocco (1938a) divided his material for the United States into three similar categories. His figures were 1055.9, 1054.4, and 1053.8 males per 1000 females born in cities, incorporated places (2500-10,000 population), and rural districts respectively. Although this trend was the reverse of that found in most other studies, the differences were statistically insignificant. Russell (1936) adversely criticized the study of Vigor and Yule, and presented English statistics to show that decreasing urbanity is associated with increasing masculinity. This author supported his conclusion with United States statistics for the years 1927-1929, obtaining an urban sex ratio of 1057 ± 1.20 and a rural ratio of 1064 ± 1.15 . Ciocco, in turn, believed that Russell's second figure resulted from a computing error, since his own computations based on the same material yielded sex ratios of 1057.2 ± 1.2 and 1057.6 ± 1.1 for urban and rural districts.

The bulk of the writings indicate that in a general population a high social and economic status is accompanied by a greater proportion of male births than is a low status. Also rural areas demonstrate a higher masculinity than urban districts, at least with respect to European countries. It is quite probable that part of the variation has its basis in differential rates of prenatal mortality, as has frequently been maintained. Bertillon (1875), Alberti (1934), and Taussig (1936) demonstrated that the incidence of reproductive wastage is higher for urban than for rural populations, and thus lend support to this explanation. These studies pertained to European data. Ciocco reported that this same condition exists in the United States, but alleged

that since he found no sex ratio differences according to urbanity in this country, the conclusion that such differences are primarily a function of prenatal mortality is subject to question.

ILLEGITIMACY

Lewis and Lewis (1906) found that in France, Belgium, and the British Isles the sex ratio of births from legitimate unions exceeded the ratio from illegitimate unions. A study by Heape (1908a) of the proportion of sexes produced in Cuba showed the same relationship. The legitimate and illegitimate matings resulted in ratios of 107.6 and 102.32 respectively in a total of 281,232 white births. The colored sex ratios were lower, but an even greater difference existed between legitimate and illegitimate births. Sadler (1830), Darwin (1871), Düsing (1884), and Bertillon (1896) had earlier commented upon this variation.

An immense amount of data dealing with this problem was amassed by de Jastrzebski (1919). The ratios covered roughly the period 1906-1915 for twenty-three countries. In the main the masculinity of legitimate was higher than that of illegitimate births, the exceptions being Norway, Sweden, Scotland, Spain, and Uruguay. England and Wales, Australia, and Denmark had approximately equal ratios in the two groups. Russell's (1936) figures for England and Wales, 1911 to 1930, showed only slightly higher sex ratios among legitimates, the differences being statistically insignificant. Ciocco reported similar insignificant differences in the United States. He maintained that figures tending to show a low sex ratio for illegitimate births in this country are the results of the racial composition of population, since about 50 percent of the illegitimate births are colored. Srdinko (1908), who found that

the masculinity of legitimate births in Austria was lower than that of illegitimates, explained this as an effect of the composition of the population. Jews in Austria contributed a small share to the total reproduction, but, according to Srdinko, a large share to the illegitimate births. As the masculinity of Jews is reported to be high (Lagneau (1882), Lewis and Lewis (1906), de Jastrzebski (1919)), the illegitimates in that country would necessarily have a high ratio. The validity of such an assertion is perhaps questionable since illegitimate births among Jews have been shown by Lagneau and by Pearl (1939) to be relatively rare as concern Prussia and Russia in the former case and the United States in the latter. The most logical explanation of the variation in sex ratio between legitimate and illegitimate births is a difference in the incidence of reproductive wastage due to both natural and artificial terminations of pregnancy. The difficulty of obtaining accurate data on either abortion or illegitimacy is considerable, and trustworthy figures combining these are well-nigh an impossibility. However, a high proportion of conceptions resulting from illicit unions undoubtedly terminate in abortions. Bertillon (1893) gave data for Paris and Saint Étienne which showed higher rates of abortion among illegitimates than among legitimates for each month of pregnancy except the ninth.

It might be thought, from a superficial consideration, that there could be no selection for sex in criminal or therapeutic abortions, but actually in view of the difficulties of inducing terminations of pregnancy (Pearl, 1939) such a selection is not an impossibility. If the constitutional make-up of the male embryo is such that it is more susceptible to natural abortion, there is no reason to believe that it is not also more susceptible to induced

abortions, commonly resulting from illicit unions.

Order of birth

The variations in sex ratio associated with social conditions are sometimes ascribed to differences related to order of birth or age of parents. There is almost complete agreement that the sex ratio decreases with increasing parity. Lewis and Lewis (1906) found that masculinity of first births exceeded that of subsequent births in Scotland. When the material was classified according to birth order there were irregularities which the authors ascribed to the meagerness of the numbers, especially for later pregnancies. The figures for Budapest, reported by de Jastrzebski (1919), are 1051 males per 1000 females among first births and 1049 for later births. Savorgnan (1933) found the ratios of first and successive births to be 1059 and 1054 for Italy, 1074 and 1068 for Prussia, and 1069 and 1062 for Holland. Punnett (1904) presented data showing a regular decrease in sex ratio with advancing parity. This was supported by Siegel (1917), Parkes (1924b), and Ciocco (1938a). The most common belief is again that this is due to a difference in reproductive wastage. Supposedly the reproductive mechanism of mothers who have had a number of pregnancies is less fit than that of mothers who have had few conceptions. Alberti (1934) alleged that in Milan the incidence of abortion decreased with increasing order of begetting. He stated that this resulted probably because later births were carried on only by those women who were physically most fit and free from pathological conditions. However, Pearl (1933) showed an increase in the rate of abortion with increasing number of pregnancies of a selected group of highly fertile women. Hence there may be two factors concerned in

abortivity in relation to order of gestation; first, a selection of women which tends to reduce abortions of later gestations and second, an increase in prenatal mortality, as a consequence of previous pregnancies. The findings of Alberti were detrimental to the theory that masculinity according to parity is a function of prenatal mortality, but no definite conclusion can be drawn from this single unsupported investigation. Huntington (1938) discussed the problem at length and maintained that the rate of abortion is a factor of prime importance. He based his conclusion on Kopp's (1933) confirmation of Pearl's observation that the incidence of spontaneous abortion increases with rising order of pregnancy. Huntington also believed that birth rank might have some influence on the germ cells and thus affect the sex ratio at conception.

There is a paucity of data on the sex ratios of birth orders among lower animals. Sumner, McDaniel, and Huestis (1922) found no differences in sex ratio according to litter order of *Peromyscus*. King (1924) reported that in rats the sex ratio gradually increased from 103.6 in the first and second litter groups to 141.6 in the ninth and tenth litter groups. After this there occurred a sharp decline. Although no statistically significant differences were found between successive litters, King believed that this lack was outweighed by the similarity in trend shown by four groups of rats, albinos, piebalds, extracted albinos, and extracted Norways. Obviously these studies are not consonant with the human material. Johansson (1932) reported a high sex ratio in first-born cattle, lower in second and third births, and an increase with later births. His figures indicated that the variations were due to differences in reproductive wastage.

AGE OF PARENTS

Sadler (1830) considered the sex ratio to be regulated by Divine purpose in such a manner as to insure maintenance of the population. According to his view, if, in a certain group, men married women much younger than themselves, many women would be left celibate and therefore unproductive. In such cases a law of nature would increase the proportion of males at birth so as to compensate for the greater amount of male mortality due to the difference in the age at marriage of the two sexes. *A posteriori* considerations first led Sadler to assume that his theory was valid. He postulated that in urban marriages and in illegitimate unions the males and females were nearer the same age than in country and legitimate matings. Since his data showed low sex ratios of city offspring and of illegitimate offspring, the allegation was made that matings between parents of the most equal ages led to the lowest sex ratios.

Attacking the problem from another angle, Sadler presented statistics from peerage registers which showed an increase in the proportion of male births corresponding to an increase in the excess of the age of the father over that of the mother. Since there was a total of only 381 marriages, and these divided into seven age groups, it is obvious that the basis of the proof was gossamer. The same theory was upheld by observations of Hofacker (1827), and it existed for over half a century. Kisch (1887) suggested a modification of this Hofacker-Sadler law to conform with his own observations from data on European royalty. He believed that there was a marked increase in male births only if the husband was at least ten years older than the wife, and she at the height of her reproductive activity (20-25 years). Further figures on royal births (Wall, 1887) failed to

conform with Sadler's observations, inasmuch as when the father was the older parent the sex ratio was 96.5 and when younger 119.2. Wall alleged that when males married later in life the masculinity of the offspring was low, and he attributed differences among social classes to this cause. It is difficult to see, from the irregularity of his figures, how he could have arrived at this conclusion. Other and more extensive investigations have resulted in complete abandonment of the so-called law. An early study by Stieda (1875) first cast suspicion as to its validity. Lewis and Lewis in their investigation discredited any association between masculinity and the relative ages of parents. Analysis of 1,436,762 Austrian births by de Jastrzebski revealed a sex ratio of 105.5 when the father was the older, and 105.7 when the mother was the older. Among more recent studies, Ciocco (1938a) reported insignificant variations in sex ratio according to relative ages of parents, while an examination of Russell's (1936) table likewise shows no association.

The general relationship which exists between age of parents and birth order of the progeny would suggest that there might be a decrease in sex ratio associated with an increase in the absolute ages of the parents. Sadler's material failed to show such a relationship and those of Wall and of Kisch were equally irregular. Because of the small number of births in each of these studies, not much weight can be attached to the results. Lewis and Lewis examined the sex ratio of several European countries and found no regularity of increase or decrease with advancing age of parents, either separately or combined. Other evidence has shown that whatever relationship may exist is in the direction of a decline in masculinity with increasing age. Lagneau stated that this was the

case, although he gave no figures to support his belief. Specht (1916) found a high sex ratio for children of young mothers. Hospital maternity cases were divided by Parkes (1924b) into five-year age groups. The 8384 births demonstrated, by and large, a decrease in sex ratio from 119.8 in the 18-22 year age group to 84.6 in the 43+ group. The youngest age, 13-17, with a ratio of 163.8, contained too few cases to be considered representative of that class. Ciocco (1938a) found no consistent trend in the sex ratio according to a quinquennial age distribution of parents. However, when a dichotomous division at 30 years

general comments apply here as in the discussion of parity. Parkes (1924b) reported a steady increase in the incidence of abortion and of stillbirth with increase in the age of the mother, concluding that this is responsible for the decline in sex ratio. If this is the case, the frequently observed decline with increasing age of the father must also be accounted for. The obvious suggestion is the correlation which exists between the ages of husbands and wives. Although data are almost entirely lacking on this point as concerns masculinity, a comprehensive report by Yerushalmy (1939) on stillbirths, sheds some light on the problem. This author

TABLE 5

Sex ratio of births and age of fathers and mothers, United States B.R.A.

(From Ciocco, 1938a)

PARENT	AGE	1917-19	1920-24	1925-29	1930-34
Fathers	Under 30	1059.2 $\pm$ 1.6	1061.2 $\pm$ 1.1	1061.3 $\pm$ 1.0	1058.1 $\pm$ 1.0
	Over 30	1057.4 $\pm$ 1.4	1054.4 $\pm$.9	1056.1 $\pm$.9	1053.3 $\pm$.9
Mothers	Under 30	1058.5 $\pm$ 1.3	1059.8 $\pm$.9	1060.7 $\pm$.8	1057.4 $\pm$.8
	Over 30	1057.6 $\pm$ 1.8	1052.8 $\pm$ 1.2	1054.0 $\pm$ 1.1	1052.3 $\pm$ 1.2

of age was made, the ratios of Table 5 resulted.

The measure of dispersion used in Table 5 is the standard error. Except for the years 1917-1919 the sex ratios by age for each parent differ by an amount which is statistically significant. Russell's data for the same country showed a similar relationship for fathers, but no consistent decline by five-year age groups of mothers.

The majority of the above studies suggest no explanation for the differences observed. The theory has been offered that the decline in masculinity according to advancing age is associated with increasing parity. This is merely side-stepping the issue as to what may be the causal factors of both phenomena. Concerning reproductive wastage, the same

found the following stillbirth rates per 1000 total births for the United States in the years 1931 to 1935.

		Age of parents								
		UNDER 20	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55 AND OVER
Father.....	40.1	33.1	28.8	30.0	35.7	43.3	48.8	52.3	52.3	
Mother.....	38.4	30.4	29.9	31.8	45.9	60.1 (40 and over)				

These figures were based upon totals of 391,648 stillbirths and 10,590,775 live births. The data of Bertillon (1896) demonstrated a similar trend in the incidence of abortion with increasing ages of women.

The decline which occurs in the early

ages is not in conformity with the observations of Parkes on a much smaller body of data. In this respect the figures of Yerushalmy and Bertillon fail to account for any regular decrease in masculinity from the youngest to the oldest ages, but the higher stillbirth and abortion rates in the older age groups may be sufficient to account for differences in the sex ratio when a dichotomous division is made. Yerushalmy found that when each age of either parent was held constant, the stillbirth rates according to the ages of the other parent still showed the same U-shaped distribution. Since the stillbirth rates may change with the age of the father, quite independently of the age of the mother, this suggests that there may be changes with age in the quality of the spermatozoa. While it appears that changes in the incidence of reproductive wastage may account in part for the higher masculinity of progeny of both fathers and mothers who are over thirty years of age, irrespective of the correlation between their ages, it is by no means certain that the sex ratio of conception exerts no influence. Bonnier (1926) reported that fathers under 38 produced 51.30 percent male offspring, and those over 38 produced 53.06 percent males. He alleged that the causal factor in this case was an alteration in the primary sex ratio.

Goehfert (1882) observed that the sex ratio of foals was 89.8 from mares under 10 years of age and 93.9 from mares over 10 years. Stallions in the same age groups produced ratios of 77.9 and 105.5 for the young and old ages respectively. Johansson (1932) found only insignificant variations in the sex ratios of cattle with advancing ages of the parents.

King (1924) investigated the relation between age and sex ratio of rats, basing her conclusions on litter order rather than on age itself. Up to the fifth litter,

which included parent rats from three to seven months old, the ratio was 103 males to 100 females. The proportion of males steadily increased through the tenth litter, or to parental ages of twelve or fourteen months. After this point there occurred a sudden drop to a sex ratio of 75 at the time when the rats were approaching the menopause. King maintained that physiological factors undoubtedly determine this change with the age of the mother, and suggested that a higher rate of mortality of very young foetuses may have caused the sudden drop at old ages. In another paper (1921) this author alleged, from a small number of cases, that very young rats (averaging 99 days) and old rats (over 15 months) cast litters containing a markedly higher proportion of stillbirths, than did mothers of intermediate ages. Since in rats, as in man, the sex ratio of stillbirths is higher than that of live births, the greater incidence of stillbirths among very young and very old mothers may partially account for the lower sex ratios in these groups.

TIME OF CONCEPTION

Another theory which fired biological interest was that of Thury (1864). He claimed that eggs fertilized shortly after ovulation resulted in female offspring, whereas later fertilization produced males. By thus regulating the time of service during heat, it was maintained, animal breeders could produce either sex at will. Thury cited 29 matings among cattle in which this was carried out with complete success. Clearly the paper had no statistical value. A number of equally inadequate reports on cattle were brought forth during succeeding years. The first figures of any magnitude were presented by Pearl and Parshley (1913). From a total of 480 calves, those resulting from conceptions early in heat had a sex ratio

of 98.4, in the middle of heat 115.5, and late in heat 154.8. It was quite obvious that Thury's original postulation as to the infallibility of the system of determination was false. Pearl's data supported the idea only insofar as it showed increases in the ratio of males to females. This author considered the problem to be of sufficient practical importance to merit further investigation. The subsequent study (Pearl, 1917a) on 1313 calves revealed that the sex ratio of offspring was unaffected by the time of service. The percentages of males were 51.0, 51.7 and 46.9 for the early, middle and late fertilizations, respectively. Apparently the earlier figures were based on insufficient data. The problem was further investigated by Cooley and Slonaker (1925) in the albino rat. These writers considered Pearl's study as inadequate in the method of determining the stage of the oestrous period, which was left largely up to the breeders. To overcome this difficulty a vaginal smear technique was used. In 72 copulations early in the period a sex ratio of 114.6 was obtained among the offspring. The late matings, numbering 65, yielded a ratio of 110.5. The difference was considered as insignificant.

In early studies Thury's hypothesis was brought forward as the cause of high sex ratios observed in Jewish statistics. Mosaic law forbids coitus within seven days after the cessation of the menstrual period. If conceptions early in the cycle resulted in a low proportion of males, and later conceptions in a high proportion, Jews should demonstrate a high ratio. This was put to a statistical test by Pearl and Salaman (1913). A small but accurate collection of data revealed a sex ratio of 105.4 in 415 births from parents who adhered strictly to the teachings of their religion. These authors discussed the reasons for believing that high sex

ratios generally observed in Jewish births are due to faulty registration among these people. This view was upheld by Huntington (1938) in a recent investigation.

Siegel (1916, 1917) reported that conceptions which took place 1 to 9 days after menstruation resulted in 80 percent male children, 10 to 14 days in 43 percent, 15 to 23 days in 19 percent. The study was based on 180 births resulting from conceptions which reportedly took place when German soldiers were home on limited leaves of absence. Since it is difficult to see how the figures could be prejudiced by any lack of integrity of the German women during those trying times, the only justifiable criticism is in the scantiness of the data. In view of the difficulty of determining exactly when fertilization takes place, meager statistics appear to be an almost necessary attribute of studies on this problem. Fürst (1916) found 76 percent males resulting from 49 conceptions which allegedly occurred within the first four days after menstruation. The 144 conceptions during the remainder of the cycle gave rise to a sex ratio of 45 percent males. Pryll (1916) concluded that the proportion of males showed no significant variation with the time of fertilization. His figures were 55.1 percent, 52.7 percent, and 51.5 percent for early, middle, and late conceptions, respectively, in a total of 581 births.

It was at one time thought that changes in the sex ratio during the catamenial period were due to the degree of maturation of the ova at the time of fertilization. This view was prompted by the observations of Hertwig (1905) and others on the different proportions of sexes resulting from fresh and stale frog eggs. It is only within later years that light has been thrown on the relation between menstruation and the time of ovulation,

the findings indicating that the egg is shed generally about the fourteenth day. Further recent advances indicate that because of the short duration of life of the germ cells, the time of possible fertilization is limited to a day or two (Hartman, 1939). It is evident that the earlier writers had little or no basis for attributing human sex ratio variations to the degree of maturation of the ova.

Reed (1913) alleged that ova alternate between negative and positive phases, and fertilization merely checks this rhythm in one of the two periods. If it occurs in the negative period the offspring will be female, and if in the positive they will be male. These phases, it was claimed, are six hours in length, corresponding to the ebb and flow of tide in the particular locality. Reed argued that this was a carry-over from our aquatic ancestors which were active during the flow and inactive during the ebb. Accordingly, if one were to consult the tide table for his locality (or if it be an inland region, compute what the tide should be if there were a tide) he could produce either male or female progeny at will. There are several objections to the theory, the most obvious being how to account for multiple births of opposite sexes in man and other animals. Reed mentioned that his theory worked in a score or more of cases. King (1909) tested the theory in 651 toads, showing conclusively that it fails to hold for *Bufo lentiginos*. Reed's theory, and others which claimed variations in sex ratio with time of conception during the sexual cycle, may be relegated to the class of untenable assertions.

SEASONAL VARIATIONS

The hypothesis that there are definite seasonal fluctuations in the proportions of the sexes dates back as far as Aristotle,

who advised that the most propitious times of conception for obtaining female offspring were during the periods which now correspond to the dates September 22 to October 23, and January 21 to February 19. The thing which stamped his observation as pure fiction is that these conceptions must take place in the wane of the moon. Some recent investigators have reasoned that just as lower animals demonstrate definite breeding seasons, man and his domesticated beasts may in some way retain a remnant of this which finds expression in sex ratio variations. Others have investigated the possibility of seasonal changes in masculinity without offering any theory as to how they may have arisen. Parkes (1924c) showed that the sex ratio of the albino mouse was higher from March to June than from July to October, the earlier period being the time of greatest breeding activity. The same author (1926b) later found the highest sex ratio for the albino mouse in the months October–December (55.9 percent) and the lowest in April–June (48.2 percent) for 1772 births. In *Peromyscus*, Sumner, McDaniel, and Huestis (1922) reported the ratios 104.23 for February–April; 91.48 for May–July; 102.29 for August–October; and 85.21 for November–January. The two studies are in marked disagreement for the winter months. The report of King and Stotsenburg (1915) showed the high sex ratio of 117.7 for the period June–August, and the low ratio of 99.0 for March–May. The other two quarters each had a masculinity of 105.3, the total number of rats being 7619. The authors pointed out that the highest sex ratio was in the spring when the rats were at their greatest breeding activity, while the lowest proportion of males occurred at a time when the animals were not in their best physical condition. It was suggested that metabolic changes in

one or both parents might be the cause of the seasonal fluctuations, the metabolic changes in turn resulting from environmental variations. The results of Hanson and Sholes (1924) on the albino rat were antithetical to those of King and Stotsenburg, although the seasonal differences were insignificant. Curiously, all of the ratios showed an excess of female births.

According to Heape (1908b), records on dogs revealed a greater sex ratio during the winter than in the summer. He associated this with the low birth rate during the cold months. Whitney's (1939) study on German Shepherd dogs was in accord with the observations of Heape. In 1440 offspring the sex ratio was 116.1 for the period June to November, and 143.1 for the remaining months.

In an excellent investigation of the sex ratio of cattle, Johansson (1932) found no seasonal fluctuation for two breeds, despite a greater incidence of reproductive wastage during the summer months. In the cow the male foetus is more subject to stillbirth and abortion than is the female. Parkes (1926c) was unable to find any seasonal changes in the masculinity of 10,961 Duroc-Jersey pigs. The maximum and minimum quarterly ratios differed by only 1.7 percent. Over half of the births occurred in the March-May period. Further lack of seasonal variation was noted by Jull (1924) and by Lambert and Curtis (1929) in studies on the domestic fowl.

In man, Lewis and Lewis (1906) could detect no regular progression in masculinity which would suggest any definite seasonal change. Moreover, the maximum ratios for several groups of people occurred in different months, and likewise the minimum ratios. Bonnier's (1924) analysis of Swedish statistics gave results which were in accord with those of Lewis and Lewis. Ciocco (1938a) observed that the monthly oscillations in sex ratio dur-

ing two quinquennial periods for the United States could easily be due to chance. The ratios in each period were based on totals of over ten million births.

The quarterly sex ratios found by Russell (1936) showed no significant differences for England and Wales, but were held to suggest that in the United States the summer months appeared to be more favorable for the production of male births.

Heape (1908a) presented data which purported to show that there are definite breeding seasons in Cuba, and that there are also seasonal fluctuations in sex ratio, the two being inversely related. The figures are presented in such a way as to make the association more apparent than real. Heape gave the months of highest and lowest birth rates and the sex ratios for these months, failing to list the sex ratios for the remaining periods of the year. He made six such comparisons, white and colored births for the years 1904, 1905, and 1906, which were intended to show high masculinities associated with low birth rate, and vice versa. One of these (colored, 1905) revealed the opposite situation. In another (whites, 1904) the total sex ratio for the year exceeded that for the month of lowest birth rate, showing that another month or months had an even greater ratio. In yet a third (colored, 1906) the total sex ratio for the year was lower than that for the month of highest birth rate, proving that another month or months had a still lower ratio. If, in Heape's study, there is actually an inverse relation between seasonal birth rate and seasonal sex ratio, he chose an unfortunate method of presenting the data. Bonnier also criticized Heape's analysis, and he demonstrated that in 2,316,321 Swedish births there was a seasonal fluctuation in birth rate but this was in no way related to mas-

culinity, the correlation coefficient being $-.020 \pm .07$. It was Huntington's (1938) belief that low sex ratio was associated with many births, both occurring during a season of good climate and high reproductive vigor of the parents. Although the discussion suffered not at all from any attempt at brevity of statement it failed to carry with it any great amount of statistical conviction.

It is quite certain that seasonal fluctuations in masculinity occur among mice and rats although the experiments are not always in accord. Among domesticated animals such variations are lacking. In man there is a diversity of opinion among students, but the greater amount of evidence indicates that there is no association between sex ratio and season. Parkes (1926c) concluded that those animals which have most marked breeding seasons likewise show seasonal oscillations in masculinity, and the greater the tendency toward domestication or artificial conditions the less will be the seasonal fluctuations in the sex ratio.

ANNUAL VARIATIONS

Little has been published on annual variations in sex ratios for animals lower than man, and what information does exist covers usually only two or three years. Jull's (1924) figures for the domestic fowl showed a slightly higher percent of male births for the period 1920-1921 than for the preceding and succeeding two-year periods. The writer believed that this was due to the small number of parents in the middle group. Sumner, McDaniel, and Huestis (1922) found widely divergent sex ratios in *Peromyscus* over the period 1915-1921. Several of the differences were statistically significant. A study of mice by Parkes (1926b) showed no statistically significant annual fluctuations over a four-year period. In

the albino rat King and Stotsenburg (1915) reported a sex ratio of 108.1 in 1914 and 106.9 in 1911-1913 in a total of 7619 offspring. Despite the large amount of data on sex ratios extracted from the herd books, little or no attention is given to yearly oscillations. There has been considerable diversity in sex ratios presented for domesticated animals by various writers whose data were based upon different years, but no significance can be attached to this in view of the non-conformity of breeds and other factors which may influence the proportions of the sexes.

Gini (1908) tabulated quinquennial sex ratios of human births for all European countries and a few in Africa, Asia, Oceania, and the Americas during the nineteenth century. Among the most complete of these, Norway, Sweden, Finland, and Spain showed gradually increasing ratios, while those of Scotland, England and Wales, France, Rumania, and British India were on the decline. Others remained relatively constant or else extended over too short a period to show any definite trend. The figures reported by Lewis and Lewis (1906) are in agreement with those of Gini. It was shown in this study that although a decline in masculinity might accompany a decline in birth rate as in the case of France and Scotland, the correlation did not always exist. Concerning this problem, Wolda (1927) concluded from his study of yearly changes in Sweden and Holland that a positive relationship existed between sex ratio and rate of conception. Russell's (1936) analysis of annual variations in sex ratios and birth rates for England, 1875-1932, revealed a correlation coefficient of $+0.216 \pm 0.126$. When the data were divided according to the degree of urbanization, the coefficient was negative for London and for country boroughs, and positive for small urban

districts and for rural districts. All of these were statistically of less significance than the coefficient of correlation for the entire country.

Most of the investigations of annual fluctuations have been made with a view toward determining whether or not social upheavals influence the sex ratio. Düsing (1884) reported an increase in masculinity in Sweden following the war with Russia in 1789 and 1790. Lewis and Lewis were cautious about drawing any conclusions, but suggested that war recovery years might show an increased ratio, while recovery from epidemics might show a decreased proportion of male births. Gini believed that the rise in sex ratios during or shortly after wars was only coincidental. He found no visible trace of increase for the belligerent countries in the war of 1870 and 1871. The same author was unable to discover any significant annual variations as a result of a cholera epidemic in Italy, 1865-1866, or as a result of famine in India during the final years of the last century. Nixon (1916) studied the statistics of France, Prussia, England, Belgium, and Holland from 1863 to 1877 and agreed with Gini that there was no perceptible rise in masculinity shortly before, during, or after the Franco-Prussian War. He likewise found no significant increase or decrease in London, England and Wales, or Scotland in 1913, 1914 or 1915, as compared to previous years. The latter part of the investigation was too premature to justify any conclusion as to the effect of the World War. Mallet (1918), who had in addition the 1916 figures for the same countries, believed that the increase of the 1915 and 1916 ratios over those of the average for 1894 to 1913 could not be dismissed as accidental. The differences were not tested for significance. Similar observations, extended through 1918, led

de Jastrzebski to agree with Mallet that the war raised the masculinity in the British Empire and also in Hungary, Finland, Switzerland, Denmark, and the Netherlands. Savorgnan (1921) observed that although there was a high sex ratio for England and for Germany during the war, it was even higher in 1919. He attributed the increase to a better condition of the mothers, which supposedly resulted from the infrequency of pregnancies during the war period. Ciocco (1938a) objected to this explanation on the grounds that the proportion of male births also increased in neutral countries where there was no prolonged absence of the husbands. Russell (1936) reported the mean sex ratios for twelve belligerent and seven neutral countries in the periods 1915-18, 1919-20, and 1921-23. For each nation the ratio of the middle period was highest. Mean numbers of males per 1000 females for all belligerent countries were in order, 1058, 1069, and 1058, and for neutral countries 1061, 1067, and 1062. A more detailed study by the same writer on England and Wales showed a much greater excess of males during 1919 than in the preceeding or following years. Russell suggested no reason for this rise during the demobilization period. For the United States, Ciocco presented annual sex ratios from 1915 to 1934. The data showed no fluctuations during war time which could not be attributed to chance. Ciocco further pointed out that there occurred no increase in masculinity coincident with the depression years following 1929.

An adequately supported theory has yet to be advanced to explain the increased sex ratios of European countries during and shortly after the World War. Curiously the increase occurred in spite of the higher incidence of reproductive wastage during those years. Bluhm (1921) stated

that among working women in Germany, 1915-1916, the rate increased to as high as 190 abortions for every 100 live births. Bayer (1938) reported that abortions increased during the war years in Germany by four to ten percent, but he believed these figures to be much too low. Inasmuch as the sex ratio increased for neutrals as well as for warring nations, the possibility suggests itself that a nutritional factor was at work. Bayer claimed that the German population which remained at home in communities of less than 2000 did not suffer the privations of the war. Nevertheless the sex ratio increased in such districts, a fact which he alleged resulted from conception by undernourished fathers who had returned from war duty. He believed that this supported the theory that inadequate diet is injurious to spermatozoa. The truth of the assumptions which Bayer made is clearly open to question.

NUTRITION

A few studies on the influence of nutrition have already been mentioned in the section concerning theories of sex determination. Since the food intake in man is not subject to control, allegations that the quantity of nutrition or quality of nutrition is responsible for human sex ratio differences have been mainly speculative. Düsing (1884, 1891) believed that undernourishment caused an increase in masculinity whereas plenty of food resulted in the opposite effect. Punnett (1904) recognized the limitations of studies on human populations. He found that the wealthier classes in London produced a higher proportion of male children than the poorer classes. This, he suggested, would indicate that better nourishment increased the sex ratio. However, after investigating the effect of other factors such as fertility and age of parents,

which are also potentially related to sex ratio and economic classes, Punnett concluded that nutrition exerted little influence. Heape (1908a) upheld Düsing's claims against those of Punnett, although he contributed no statistical support from his own data. His belief that the influence of the male was negligible in problems concerning the sex ratio (he considered the female to be heterogametic) colored his thoughts on the subject of nutrition. Inasmuch as the "female-producing ova" suffer more from insufficient food than the "male-producing ova", according to Heape, the essential factor in nutrition is not merely the amount or quality of the food supplied to the mother, but her ability to transmit this nourishment to the ovary. We now know that if nutrition does influence the sex ratio its method of action must be somewhat different from this. So far as the nutrition of the female reproductive system is concerned, the effect, if any, would probably be one of differential elimination in the sexes of the embryos or foetuses. It is more likely that the quantity and quality of food supplied to the parents would influence the sex ratio only insofar as it affects the general health and vitality of those parents.

Probably because breeders hesitate to hazard the economic value of any considerable number of domesticated animals, the only available data on radical dietary changes deal with laboratory forms. Holmes (1910) starved *Drosophila ampelophila* for five generations and found no influence on the sex ratio of 4,733 offspring of the sixth generation. Further starvation up to the tenth generation yielded the same result, the ratio being approximately 90 females to 100 males in 9874 flies. Morgan (1911) mentioned that a long series of experiments on the addition of different sugars, salts, acids, and al-

kalies to the food failed to induce any alteration in the sex ratios of *Drosophila*. Schneider (1940) found that the sex ratios of progeny from thyroid-fed *Tribolium confusum* were not significantly different from those of the controls. The influence of nutrition on mice was investigated by Schultze (1904). Prolonged and rigorous restriction of the diet failed to produce variations sufficient to prove that the sex ratio had been altered by the privation, but the number of cases in the study was small. Sumner, McDaniel, and Huestis (1922) reported a masculinity of 104.31 ± 9.31 for 237 offspring of mice which had been fed an excess of proteins. The 228 births from mice which received normal rations had a sex ratio of 95.56 ± 8.61 . The difference is far from being statistically significant. Slonaker and Card (1923) studied the sex of progeny from albino rats which had been on restricted diets. The sex ratios of offspring from five groups of undernourished parents were 84.0, 86.0, 90.0, 97.0, and 116.0. A total of 385 offspring of restricted feeders had a sex ratio of 95.5 as compared to 108.0 for 1001 births from matings of normal feeders. The writers concluded that the general effect of diet limitation was to decrease the proportion of male births. No explanation could be given for the excessively high rate of 116.0 in one group.

Parkes and Drummond (1925) reported a sex ratio of 44.6 ± 2.02 in the offspring of male rats which had received a diet containing two percent or less of yeast extract, and a ratio of 49.2 ± 1.96 in offspring of male parents which had received three percent or over of yeast extract. The difference relative to its probable error was 1.64. The writers considered this to be a small but significant difference. During the first eight weeks of the diet deficient in vitamin B

the sex ratio of progeny was 49.1 ± 2.31 and during the next twelve weeks, 44.2 ± 2.04 . The difference divided by its probable error was 1.6, and this again was considered significant. The writers maintained that a deficiency in vitamin B lowered the sex ratio in proportion to the duration of the deficiency. They attributed this effect to an alteration of the spermatozoa rather than to any difference in prenatal mortality. Although the figures tend to show the relationship claimed, the differences, when considered statistically, are not sufficient to warrant any definite conclusion. The same authors (1926) found that the offspring of rats which had been subjected to vitamin A deficiency had sex ratios that showed little variation from the normal.

Hoelzel, DaCosta, and Carlson (1939) reported the following sex ratios for cross-matings of rats which had been fed low protein (7.5-12 percent casein) and high protein (30-50 percent casein) diets.

TYPE OF MATING	NO. OF OFF-SPRING	SEX RATIO
Low protein ♂ × high protein ♀..	420	107
High protein ♂ × low protein ♀..	553	145

The diets of the parents in the second group were later reversed, and the 455 progeny had a sex ratio of 92. The authors alleged from this that the better nourished parent had a tendency to determine the same sex in the offspring. The hypothesis was advanced that the state of protein metabolism induced in the well-nourished parent affects the germ cells and enhances the survival value of embryos of the same sex. The divergence of the sex ratios was thus ascribed to sex-differential resorption of embryos. Unfortunately, there is no record of the age of the parents, which itself may influence the ratio, although it was stated

that age deterioration had not set in. Contrary to the writers' statement, a diet high in protein content does not imply better nourishment. An excellent series of experiments by Slonaker (1939) showed that a diet of about 14.2 percent was most efficacious for the physiological functions of rats. The percentages of protein in five diets, otherwise the same, were I, 10.3; II, 14.2; III, 18.2; IV, 22.2; and V, 26.3. Diets I and II were definitely superior for all of the reproductive functions of the parents, showing the least amount of sterility, the greatest average number of young born, the youngest average age at birth of first litter, the oldest average age at birth of last litter, and the greatest reproductive span. As to the average life span, the order of diets with decreasing longevity was for males II, I, III, V, IV, and for females, I, III, II, V, IV. The sex ratios in a total of 7,933 births were I, 95.4; II, 103.6; III, 95.3; IV, 94.5; and V, 93.3. All of these ratios are below the normal for the rat. It is noteworthy that the diets which gave rise to the highest sex ratios were the same diets which resulted in the greatest reproductive efficiency and generally speaking, in the biologically fittest individuals, as indicated by length of life.

Experiments on mice and rats indicate, by and large, that nutrition of the parents probably does influence the proportion of sexes among the offspring, the better nourished parents producing a higher male sex ratio. Whether this results from an alteration of the ratio at conception, as postulated by Parkes and Drummond, or from a differential elimination of embryos, according to the views of Hoelzel, Da-Costa, and Carlson, cannot easily be determined.

No experiments have been conducted which directly relate the vitality of parents to the sex ratio of births, but such a

relationship has frequently been suggested as an explanation of other sex ratio variations. Thus King (1915) stated in connection with seasonal fluctuations in rats that the sex ratio was low when the parents were in poor physical condition, and high when in good condition. The same author (1921) found that stillbirths increased during times of low vitality. Parkes (1924a) observed that when conceptions in mice took place during a poor condition of the mothers there was a decrease in the sex ratio of the offspring, and, coincident with this, an increase in the amount of embryonic elimination. The poor condition, in this study, was the after-effect of a recent parturition. Savorgnan invoked this same principle to explain the increase in masculinity during wars. He alleged that due to the long interval between pregnancies the mothers were in better physical condition and the sex ratio was consequently increased. It is difficult to accept his hypothesis as to the fitness of the maternal organism in view of the rise in the rate of reproductive wastage during war years. If vitality of the parents actually does influence masculinity, it is much more plausible that sex ratio differences associated with age, nutrition, and social conditions are, at least in part, a resultant of this factor, either through alteration of the primary sex ratio or through differential rates of prenatal mortality.

FERTILITY

The large number of factors, environmental and biological, which influence fertility, complicate the study of any particular phase of this subject. The more important of these factors were comprehensively analyzed and discussed by Pearl (1939). In the following sections fertility will be considered only in rela-

tion to the biological variables concerned in the present investigation

Fertility and sex ratio

Amongst laboratory mammals, fertility is frequently referred to as litter size rather than as the number of offspring produced throughout life, or between certain time limits, as in the case of age specific fertility. Studies of the relationship between sex ratio and fertility in sub-human organisms are therefore not comparable to such investigations in man. Pearson found in his analysis of Weldon's (1906) data on mice that there was no individual relationship between litter size and sex ratio, but in a generation the correlation was $.63 \pm .17$. Since Pearson believed that only environmental conditions could influence either sex ratio or litter size, he concluded that when these conditions favored large litters they also favored male births. In the deer-mouse *Peromyscus*, Sumner, McDaniel, and Huestis (1922) reported a sex ratio of 94.85 ± 2.94 in broods of one to three births, and 102.42 ± 3.01 in broods of four to nine births. No regularity of increase existed when litter sizes were taken separately, and the authors believed that the difference which resulted from grouping was accidental. Parkes (1924c) gave mouse sex ratios of 83.7, 120.5 and 125.4 for litters of size 1-4, 5-8, and 9-12 respectively. In a later study (1926b) this author found no correlation between litter size and the proportion of males in 1872 births of mice. The figures compiled by King and Stotsenburg (1915) for the albino rat revealed no definite change in sex ratio with increase in litter size. Wentworth (1914) reported no relationship between these variables in 174 litters of pigs, a finding supported by Parkes (1923). Wentworth also declared that multiple births of dogs gave sex ratios which dif-

fered but little from the expected proportions. By and large these studies indicate that among normally multiparous animals there is no association between sex ratio and litter size. The exception is in very small litters of mice, which probably in many cases represent the survivors from an originally much greater number of embryos. Since prenatal mortality in mice falls predominantly on males (Parkes, 1924a), this may explain the low masculinities sometimes observed in small litters. In his early study Parkes accepted this explanation, but abandoned it upon finding no abnormal sex ratio in small litters in his 1926 investigation.

Several studies have been mentioned concerning a possible relationship between the sex ratio and the birth rate, particularly in the sections on seasonal and annual variations. The terms "fertility" and "birth rate" were used interchangeably by Heape (1908a). It should be pointed out that an association between sex ratio and birth rate does not denote any association between sex ratio and fertility, except possibly for variations between decades or longer. Geissler (1889) found in statistics of nearly one million families that in sibships of seven and less the sex ratio was 105.8 while in sibships greater than seven it was 106.8. An analysis by Willoughby (1931) of families of university students revealed correlations between fertility and sex ratio of $-.24 \pm .08$ for paternal sibships, $+.07 \pm .08$ for maternal sibships, $-.34 \pm .07$ for paternal cousin sibships, and $-.12 \pm .08$ for maternal cousin sibships. In general his data tended to show an inverse relationship, but without further confirmation the result can hardly be considered conclusive. Winston (1932) reported ratios of $54.57 \pm .53$ percent in 1-2 child families, $52.74 \pm .40$ in 3-4 child families, and $51.48 \pm .49$ in families

of 5 and over, the total number of births being 15,763. The difference divided by the probable error of the difference was, for the first and third of these ratios, 4.28; for the first and second, 2.76; and for the second and third, 1.90. Punnett's (1904) data from *Burke's Peasage* showed this same relationship. The results obtained in these studies would be expected to follow from the decrease in sex ratio which is known to accompany an increase in parity.

Darwin (1871) suggested that declining races might generally exhibit high masculinity. The theory was investigated by Pitt-Rivers (1927) who found sex ratios much higher than normal at the ages of marriage in the declining populations of New Zealand, Australia, New Guinea, and Samoa. He believed that this was largely due to a higher rate of mortality among females than among males during childhood. This is contrary to all investigations on human populations. Powdermaker (1931) made genealogical studies of New Ireland and found that 55 percent of the births were males, whereas at the ages of marriage 53 percent were males. Obviously more males than females died before marriage age in this declining population, which indicates that the high masculinity found by Pitt-Rivers was probably due to a high masculinity at birth. It is difficult to account for this high sex ratio at birth, but it may be partially due to a lower fertility in declining races.

Fertility and longevity

Inquiries into the association between fertility and length of life were initiated by a desire to know if the burden of childbirth sapped the vitality of prolific mothers, causing them to die early, or if highly productive mothers had an inherently superior vitality and were there-

fore long-lived. Beeton, Yule, and Pearson (1900) investigated the relationship from English and American genealogical records. For American fathers and mothers the fertility increased throughout the entire age range, while for English parents it first increased and then decreased slightly after a length of life of about seventy years. Inasmuch as a positive association existed even beyond the age limit of reproduction, the authors concluded that "the peculiar physique in both men and women which leads to longevity is also associated with greater fecundity." The term "fecundity" obviously was meant as fertility. The weaknesses of this study were adequately discussed by Freeman (1935), the essence of the criticism being that the mean ages of death were not representative of the entire group, that the long time period of the genealogies permitted secular variations in fertility, which might influence the results, and that no account was taken of the duration of marriage.

Powys (1901) presented data from the vital statistics of New South Wales for the years 1898 and 1899. This study supported the claims of Beeton, Yule, and Pearson in that for women the fertility reached a maximum when the age of death was 65-70 years and dropped slightly thereafter. The figures were supplemented with statistics from 1900 to 1902 (Powys, 1905) giving a total of 83,362 births from 15,548 mothers. The trend in fertility of mothers was almost identical to that of the earlier analysis. Fertility increased quite regularly throughout the entire life range of 100 years for the fathers, but Powys cautioned against attaching too much significance to the increase because of the indefinite age of sexual decline in males. A number of very high correlation coefficients were reported, but these were computed from

averages rather than from individual family sizes. As in the preceding study no account was taken of the duration or age of marriage. Bell (1918) divided age at death of parents from the Hyde genealogy into the groups under 40, 40 to 60, 60 to 80, and 80 and over. The corresponding numbers of children per parent were 2.8, 6.0, 6.9, 7.1 for fathers and 3.4, 6.2, 6.6, 7.2 for mothers. This investigation suffered all the limitations of the work of Beeton, Yule, and Pearson.

Freeman (1935) attempted to overcome earlier difficulties by limiting the time periods covered in her genealogical data, and by taking age of marriage into consideration. Seventeen correlations were made between fertility of mothers and length of life beyond 45 years. Fourteen of these were positive. The relationship was most pronounced where the women had married under 20 years of age, the coefficient of correlation being $+ .1027 \pm .0282$. Since this was probably not due to sampling error, it indicated that for women who married under 20 and died after 45 years of age, increased longevity was associated with greater production of offspring. While the remaining correlations were of lower order and could not be considered entirely beyond the range of sampling variation, they showed by and large the same associations. Dorn and McDowell (1939) using Australian statistics on 195,000 women, demonstrated the necessity of keeping year of marriage and age at marriage relatively constant. When these factors were controlled, the number of children per woman was found to increase with increasing length of life beyond 45 years. Unfortunately, due to the nature of the raw material, no valid statistical tests could be applied. In order to determine if the relationship held for women dying before the end of the reproductive period, Dorn

and McDowell compared the mean number of offspring of women who died at each age under 45 years with the mean number of offspring of women who were married at the same age and produced during the same time period, but were still alive. It was found that, except for women who died within five years after marriage, the living mothers had produced a greater average number of children during the same period of time than the women who had died. The authors believed that although the data were not entirely satisfactory, they suggested that the positive association between fertility and longevity existed among women who died during the reproductive period as well as among those who died after this period.

Although the two most recent investigations failed to show as marked an association between the variables as did the earlier studies, they nevertheless upheld the general truth of the proposition. A rational explanation of the observed relationship is that the longevous individuals, and the most fertile, are from the biologically fittest part of the population. A series of studies in human longevity by Pearl (1934) indicated that long-lived individuals are constitutionally fitter than those who die at early ages. It is likewise quite certain that physical health is a factor in fertility. Brown, Greenwood, and Wood (1920) reported that among 632 women over 18 years of age who were classified according to health, those with excellent and good health produced an average of $2.09 \pm .05$ children while those with fair, poor, and bad health had produced $1.56 \pm .10$. These women had not yet reached the menopause. The mean ages at marriage and durations of marriages were almost identical for the two groups, but no indication was given as to the distributions.

Pearl (1936) classified physical health among the more important factors which influence fertility. Constitutional fitness and physical health are not synonymous, but in all probability they are closely related. The condition of the parents may influence the vigor and viability of the germ cells, or the rate of reproductive wastage, either of which is an important element in the expression of fertility.

SUMMARY

The numerous early theories and superstitions about sex determination have been almost completely abandoned as a result of more recent scientific investigations. Among the vertebrates and higher invertebrates sex determination is primarily a genetic process taking place at the time of conception, although hormonal or environmental influences can, in certain cases, dominate the chromosomal mechanism.

The weight of the evidence indicates that factors of an inheritable nature may give rise to transmissible variations from the normal sex ratio of any particular species. Just as there are interspecific variations in the normal sex ratio of sub-human organisms, there are also variations in masculinity among the different races and nationalities in man. Many studies have indicated that cross matings result in an increased sex ratio among the offspring of both man and lower animals, a result which may be an expression of the increased vigor which commonly accompanies hybridization.

By and large a high social or economic status is accompanied by a greater proportion of male births than is a low status, and rural districts demonstrate a higher masculinity than urban areas. The most widely accepted explanation for these differences is that high social and eco-

nomic classes, and also rural inhabitants, have lower rates of reproductive wastage. Since in mammals abortions and stillbirths occur more frequently among male foetuses than among female, it has been asserted that populations with a low incidence of prenatal mortality will demonstrate a high sex ratio. This explanation assumes that there is little or no variation in the primary sex ratios of the groups under consideration, a postulate that is by no means valid for all cases. However, differential rates of reproductive wastage appear to be the most plausible explanation for variations in the sex ratios of socio-economic classes and of urban and rural groups. It likewise readily accounts for the higher sex ratio among legitimate births than among illegitimate births.

Although the relative ages of the father and mother exert no influence on the sex ratio of the progeny, it has been demonstrated that for man there is a decrease in the proportion of male offspring with an increase in the absolute age of either parent. Likewise the sex ratio decreases with increasing parity in human populations. Changes with age and parity in the rate of reproductive wastage probably account in part for the differences in sex ratio, but there may also be changes with age in the masculinity of conceptions.

Early reports that sex was determined, or the sex ratio influenced, by the time during the sexual cycle at which fertilization takes place have been disproved by more comprehensive investigations of the problem.

In lower animals, with a definite breeding season, there appear to be seasonal fluctuations in masculinity. There is little evidence that such is the case among domestic animals, and no conclusive statistical proof that seasonal

variations in sex ratios exist for man. Certain countries have demonstrated gradually increasing annual sex ratios over long periods of time, while others have shown decreases in the proportions of male births. Marked rises in masculinity occurred during and shortly after the World War among belligerent and non-belligerent European countries, but no completely adequate explanation for this has yet been offered.

The only controlled experiments on the influence which quantity or quality of nourishment has on the proportions of the sexes relate to experimental animals. The greater number of these investigations indicate that nutritional deficiencies result in a decreased sex ratio. Just how far these findings can be applied to human populations is a matter of conjecture. Attempts to analyze the problem of nutri-

tion on the basis of economic class differences have proved ineffective.

There may be a slight decrease in sex ratio with increasing fertility in man, a result which would be expected in view of the decline in masculinity which accompanies increasing order of birth.

Among parents who died beyond the period of reproductive activity, the most longevous were found to have produced, on the average, a greater number of offspring than those who were short-lived. The relationship is not as marked as was alleged by the earliest investigators, but all studies have attested to its actuality. It is suggested that the parents who were long-lived were the most fertile by virtue of their being from the biologically fittest part of the population.

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LIST OF LITERATURE

- ALBERTI, SALVATORE. 1934. La Mortalità Antenatale. *Milano* (Società Editrice "Vita e Pensiero").
- AMAR, JULES. 1929. Sexe et nutrition. *C. r. des séances de l'Acad. des Sciences, Paris*, T. 188, pp. 935-937.
- [ANONYMOUS.] 1937. The sex ratio. *Nature*, Vol. 140, pp. 958-959.
- ARISTOTILES. [n.d.] The Works of Aristotle the Famous Philosopher. *London* (Moritz and Chambers, Ltd.).
- AUERBACH, E. 1912. Das wahre Geschlechtsverhältnis des Menschen. *Arch. f. Rassen- u. Gesellschafts. biol.*, Bd. 9, pp. 10-17.
- BABCOCK, E. B., and R. E. CLAUERN. 1918. Genetics in Relation to Agriculture. *New York* (McGraw-Hill Book Co.).
- BALTZER, F. 1937. Analyse des Goldschmidtschen Zeitgesetzes der Intersexualität auf Grund eines Vergleiches der Entwicklung der Bonellia- und Lymantria-Intersexe.—Zeitlich gestaffelte Wirkung der Geschlechtsfaktoren (Zeitgesetz) oder Faktoren-Gleichzeitigkeit (Gen-Gleichgewicht). *Arch. f. Entwicklungsmesch.*, Bd. 136, pp. 1-43.
- BAYER, ALFRED. 1938. Unterernährung und Keimzellenschädigung. *Arch. f. Gynäk.*, Bd. 165, pp. 591-623.
- BERTON, M., G. U. YULE, and K. PEARSON. 1900. Data for the problem of evolution in man: V. on the correlation between duration of life and the number of offspring. *Proc. Roy. Soc.*, Vol. 67, pp. 159-179.
- BELL, A. G. 1918. The Duration of Life and Conditions Associated with Longevity. A Study of the Hyde Genealogy. *Washington* (Genealogical Record Office). Pp. 57.
- BERTILLON, J. 1875. Étude nouvelle sur les mortalités. *Jour. Soc. de Stat. de Paris*, T. 16, pp. 226-249.
- . 1893. De la mortalité par âge avant la naissance. *Jour. Soc. de Stat. de Paris*, T. 34, pp. 167-180.
- . 1896. Mortinatalité et des naissances prématurées selon l'âge du fœtus et selon l'âge de la mère. *Rev. d'Hyg.*, T. 18, pp. 473-491.
- BLUMM, AONNE. 1921. Zur Kenntniss der Gattungsleistungen der Industriearbeiterinnen im Kriege. *Arch. f. Rassen- u. Gesellschafts. biol.*, Bd. 13, pp. 75-78.
- . 1924. Über einige Versuche, bei Säugetieren

- das Zahlenverhältnisse der Geschlechter zu beeinflussen. *Arch. f. Rassen- u. Gesellschafts. biol.*, Bd. 16, pp. 1-28.
- BOLDRENT, M. 1936. La proportion des sexes dans les conceptions humaines. *Rev. de l'Inst. Internat. de Stat.*, T. 4, pp. 484-499.
- BOWMER, G. 1923. On different sex ratios in *Drosophila melanogaster*. *Zeitschrift f. indukt. Abstammungs- u. Vererbungslehre*, Bd. 31, pp. 153-169.
- . 1924. On alleged seasonal variations of the sex-ratio in man. *Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre*, Bd. 32, pp. 97-107.
- . 1926. The parental age and the sex-ratio in man. *Acta Zoologica*, Vol. 7, pp. 219-247.
- BORING, A. M., and R. PEARL. 1918. Sex studies. XI. Hermaphrodite birds. *Jour. Exp. Zool.*, Vol. 25, pp. 1-47.
- BRIDGES, C. B. 1917. The elimination of males in alternate generations of sex-controlled lines. *Anat. Rec.*, Vol. 11, p. 504.
- . 1932. Genetics of sex in *Drosophila*. In *Sex and Internal Secretions*, Edited by Edgar Allen. *Baltimore* (Williams & Wilkins). Pp. 55-93.
- . 1939. Genetics of sex in *Drosophila*. In *Sex and Internal Secretions*, Second Edition, Edited by Edgar Allen, C. H. Danforth, and E. A. Doisy. *Baltimore* (Williams & Wilkins). Pp. 15-63.
- BROWN, J. W., M. GREENWOOD, and FRANCES WOOD. 1920. The fertility of the English middle classes. *Eugenics Rev.*, Vol. 12, pp. 158-211.
- BUFFON, GEORGES. 1769. *Histoire Naturelle, Générale et Particulière*. Paris (L'Imprimerie Royale).
- CIOTTO, A. 1938a. Variation in the sex ratio at birth in the United States. *Human Biol.*, Vol. 10, pp. 36-64.
- . 1938b. The masculinity of stillbirths and abortions in relation to the duration of uterogestation and to the stated causes of foetal mortality. *Human Biol.*, Vol. 10, pp. 235-250.
- COLE, F. J. 1930. *Early Theories of Sexual Generation*. Oxford (Clarendon Press).
- COLE, L. J., and W. F. KIRKPATRICK. 1915. Sex ratios in pigeons, together with observations on the laying, incubation and hatching of the eggs. *Agric. Exper. Station of Rhode Island State Coll. Bull.* 162, pp. 463-512.
- COOLEY, C. L., and J. R. SLOWAKER. 1925. The effects of early and late breeding on the mother and the sex ratio in the albino rat. *Amer. Jour. Physiol.*, Vol. 72, pp. 595-613.
- COXE, J. R. 1846. *The Writings of Hippocrates* and Galen. Philadelphia (Lindsay and Blakiston). Pp. 159-161.
- CREW, F. A. E. 1923. Studies in intersexuality.—II. Sex-reversal in the fowl. *Proc. Roy. Soc.*, Vol. 95, pp. 256-280.
- . 1925. An attempt to disturb the sex-ratio of the mouse by continued administration of alcohol to the male parent. *Proc. Roy. Physical Soc.*, Vol. 22, pp. 89-96.
- . 1937. The sex ratio. *Amer. Nat.*, Vol. 71, pp. 529-539.
- DANFORTH, C. H. 1939. Relation of genic and endocrine factors in sex. In *Sex and Internal Secretions*, Second Edition, Edited by Edgar Allen, C. H. Danforth and E. A. Doisy. *Baltimore* (Williams & Wilkins). Pp. 328-352.
- DARWIN, CHARLES. 1874. *The Descent of Man and Selection in Relation to Sex*. New York (A. L. Burt).
- DAWSON, E. R. 1909. *The Causation of Sex*. London (H. K. Lewis).
- DONCASTER, L., and F. H. A. MARSHALL. 1910. The effects of one-sided ovariectomy on the sex of the offspring. *Jour. of Genetics*, Vol. 1, pp. 70-72.
- DORN, H. F., and A. J. McDOWELL. 1939. The relationship of fertility and longevity. *Amer. Soc. Rev.*, Vol. 4, pp. 234-246.
- DÜRING, C. 1884. Die Regulierung des Geschlechtsverhältnisses bei der Vermehrung der Menschen, Tiere und Pflanzen. *Jenaische Zeitschr. f. Naturw.*, N.F., Bd. 10, pp. 593-940.
- . 1891. Die Regulierung des Geschlechtsverhältnisses. *Int. Central. f. d. Physiol. u. Pathol. des Harn. u. Sex.*, No. 3, pp. 99-101.
- FREEMAN, BETTIE C. 1935. Fertility and longevity. *Human Biol.*, Vol. 7, pp. 392-418.
- FÜRST, C. 1916. Knabenüberschuss nach Conception zur Zeit der postmenstruellen Anämie. *Arch. f. Gynäk.*, Bd. 28, pp. 14-38.
- GALIEN. 1856. *Oeuvres Anatomiques, Physiologiques, et Médicales de Galien*. Traduit par Ch. Daremberg. Paris (J. B. Baillière).
- GEDDES, P., and J. A. THOMSON. 1889. *The Evolution of Sex*. London (W. Scott).
- GRIBLER, A. 1889. Beiträge zur Frage des Geschlechtsverhältnisses der Geborenen. *Zeitschr. d. k.-sächsischen stat. Bureau*, Dresden, Bd. 35, pp. 1-24.
- GRESHENSON, S. 1928. A new sex-ratio abnormality in *Drosophila obscura*. *Genetics*, Vol. 13, pp. 488-507.
- GINI, CORRADO. 1908. Il Sesso dal Punto di Vista Statistico. *Milano* (Remo Sandron).
- GOSWILERT, V. 1882. Ueber die Vererbung der

- Haarfarben bei den Pferden. *Zeitschr. f. Ethnol.*, Bd. 14, pp. 145-155.
- GOLDSCHMIDT, R. 1916. Experimental intersexuality and the sex problem. *Amer. Nat.*, Vol. 50, pp. 705-718.
- . 1934. Lymantria. *Bibliographia Genetica*, Vol. 11, pp. 1-186.
- GRAUNT, JOHN. 1676. Natural and Political Observations Made upon the Bills of Mortality. *London* (John Martyn).
- GREULICH, W. W. 1931. The sex ratio among human stillbirths. *Science*, Vol. 74, pp. 53-54.
- GUYER, M. F. 1909. On the sex of hybrid birds. *Biol. Bull.*, Vol. 16, pp. 193-198.
- HAMMON, F. B., and F. N. SHOLES. 1924. Seasonal differences in sex ratio, litter size and birth weight of the albino rat under uniform laboratory conditions. *Genetics*, Vol. 9, pp. 363-367.
- HARTMAN, C. G. 1939. Ovulation, fertilization and the transport and viability of eggs and spermatozoa. In *Sex and Internal Secretions*, Second Edition, Edited by Edgar Allen, C. H. Danforth and E. A. Doisy. *Baltimore* (Williams & Wilkins). Pp. 630-719.
- HARTBORNER, N. 1694. *Essay de Dioptrique*. *Paris*. (Quoted from Cole, 1930).
- HARVEY, WILLIAM. 1847. The Works of William Harvey. Translated from the Latin by Robert Willis. *London* (Printed for the Sydenham Society).
- HRAPE, W. 1907. Note on the influence of extraneous forces upon the proportion of the sexes produced by canaries. *Proc. Cambridge Phil. Soc.*, Vol. 14, pp. 201-205.
- . 1908a. The proportion of the sexes produced in white and coloured peoples in Cuba. *Philos. Trans. Roy. Soc. London*, B, Vol. 200, pp. 271-330.
- . 1908b. Notes on the proportion of the sexes in dogs. *Proc. Cambridge Phil. Soc.*, Vol. 14, pp. 121-151.
- HENKE, J. C. 1786. Völlig entdecktes Geheimnis der Natur sowohl in der Erzeugung des Menschen, als auch in der willkürlichen Wahl des Geschlechts des Kindes. *Braunschweig*.
- HERON, DAVID. 1906. On the inheritance of the sex-ratio. *Biometrika*, Vol. 5, pp. 79-85.
- HERTWIG, R. 1905. Ueber das Problem der sexuellen Differenzierung. *Verhandl. Deutsch. Zool. Gesellschaft*.
- HIGGINS, N. 1651. The History of Generation. *London* (Quoted from Cole, 1930).
- HILDEBRAND, S. F. 1927. Sex ratio in *Gambusia*. *Biol. Bull.*, Vol. 53, pp. 390-404.
- . 1933. Hybridizing diamond-back terrapins. *Jour. Hered.*, Vol. 24, pp. 231-238.
- HIPPOCRATES. 1849. The Genuine Works of Hippocrates. Translated from the Greek by Francis Adams. *London* (Sydenham, Society). Pp. 744-746.
- HOBELZEL, F., ESTHER DA COSTA, and A. J. CARLSON. 1939. Effect of protein alimentation on the secondary sex ratio of offspring of rats. *Proc. Soc. Exper. Biol. and Med.*, Vol. 40, pp. 334-335.
- HOFACKER. 1827. Ueber die Bestimmung des Geschlechts durch verschiedene Momente. *Med.-Chir. Ztg.*, Bd. 4, p. 398.
- HOLMES, C. D. 1910. The Effect of Starvation for Five Successive Generations on the Sex-ratio in *Drosophila ampelophila*. *Bull. Indiana Univ.*, No. 8, pp. 1-8.
- HOLMES, S. J. 1926. The sex ratio in infant mortality as an index of a selective death rate. *Univ. Calif. Publ. in Zool.*, Vol. 29, pp. 267-303.
- HUNTINGTON, E. 1938. Season of Birth. *New York* (John Wiley and Sons).
- HYDE, R. R. 1914. Fertility and sterility in *Drosophila ampelophila*. II. Fertility in *Drosophila* and its behavior in heredity. *Jour. Exper. Zool.*, Vol. 17, pp. 173-212.
- IBSEN, H. L. 1922. Some genetic experiments with guinea-pigs and rats. *Rec. Proc. Amer. Soc. Animal Prod.*, pp. 99-101.
- DE JASTRZEBSKI, S. 1919. The sex ratio at birth. *Eugenics Rev.*, Vol. 11, pp. 7-16.
- JOHANSSON, I. 1932. The sex ratio and multiple births in cattle. *Zeitschr. Züchtg.: B Tierzüchtg. u. Züchtungsbiol.*, Bd. 24, pp. 183-268.
- JOYET-LAVERGNE, PH. 1919. Sur les rapports entre le métabolisme et la sexualisation cytoplasmique. *C.r. des séances de l'Acad. des Sciences*, T. 188, pp. 818-820.
- JULL, M. A. 1924. The relation of antecedent egg production to the sex ratio of the domestic fowl. *Jour. Agric. Research*, Vol. 28, pp. 199-224.
- KING, H. D. 1907. Food as a factor in the determination of sex in amphibians. *Biol. Bull.*, Vol. 13, pp. 40-56.
- . 1909. Studies on sex-determination in amphibians. II. *Biol. Bull.*, Vol. 16, pp. 27-43.
- . 1910. Temperature as a factor in the determination of sex in amphibians. *Biol. Bull.*, Vol. 18, pp. 131-137.
- . 1911a. The effects of semi-spaying and of semi-castration on the sex-ratio of the albino rat (*Mus norvegicus albinus*). *Jour. Exper. Zool.*, Vol. 10, pp. 381-392.
- . 1911b. The sex ratio in hybrid rats. *Biol. Bull.*, Vol. 21, pp. 104-112.
- . 1918. Studies on inbreeding. III. The effect of inbreeding, with selection, on the sex ratio of

- the albino rat. *Jour. Exper. Zool.*, Vol. 27, pp. 1-35.
- . 1921. A comparative study of the birth mortality in the albino rat and in man. *Anat. Record.*, Vol. 20, pp. 321-354.
- . 1924. Litter production and the sex ratio in various strains of rats. *Anat. Record.*, Vol. 27, pp. 337-366.
- , and J. M. STOTENBURG. 1915. On the normal sex ratio and the size of the litter in the albino rat (*Mus norvegicus albinus*). *Anat. Record.*, Vol. 9, pp. 403-420.
- KIRCH, E. H. 1887. Zur Lehre von der Bedeutung des Geschlechtes. *Centralbl. f. Gynäk.*, Bd. 11, pp. 49-51.
- KOPP, MARIE E. 1933. Birth Control in Practice. New York (Robert M. McBride and Co.).
- [LAGNEAU.] 1882. Comparative birth- and death-rates. *Lancet*, Vol. 1 for 1882, p. 623.
- LAMBERT, W. V., and V. CURTIS. 1929. Further studies on the sex ratio in the chicken. *Biol. Bull.*, Vol. 61, pp. 226-233.
- DE LAUNAY, C.-D. 1698. Nouveau système concernant la generation. *Paris*. (Quoted from Cole, 1930).
- LAWRENCE, P. S. 1940. Ancestral longevity and the sex ratio of the descendants. *Human Biology*, Vol. 12, pp. 403-429.
- LEMNIUS, LEVINIUS. 1572. *Occulta Naturae Miracula*. Übersetzt von Jacob Horst. *Leipzig*.
- LEWIS, C. J., and J. N. LEWIS. 1906. Natality and Fecundity. *London* (Oliver and Boyd).
- LILLIE, F. R. 1916. The theory of the free-martin. *Science*, Vol. 43, pp. 611-613.
- . 1917. The free-martin; a study of the action of sex hormones in the foetal life of cattle. *Jour. Exper. Zool.*, Vol. 23, pp. 371-422.
- LINDSAY, A. W. 1932. A Textbook of Genetics. New York (Macmillan Co.).
- LISCHÜTZ, A. 1924. The Internal Secretions of the Sex Glands. *Baltimore* (Williams & Wilkins).
- LITTLE, C. C. 1919. Some factors influencing the human sex-ratio. *Proc. Soc. Exper. Biol. and Med.*, Vol. 16, pp. 127-130.
- . 1920. A note on the human sex ratio. *Proc. Nat. Acad. Sci.*, Vol. 6, pp. 250-253.
- MACDOWELL, E. C., and E. M. LORD. 1925. The sex ratio in litters of mice classified by the total amount of prenatal mortality. *Proc. Soc. Exper. Biol. and Med.*, Vol. 22, pp. 389-390.
- , and —. 1926. The sex ratio of mice from alcoholized fathers. *Proc. Soc. Exper. Biol. and Med.*, Vol. 23, pp. 517-519.
- MALLAT, B. 1928. Vital statistics as affected by the war. *Jour. Roy. Stat. Soc.*, Vol. 81, pp. 1-36.
- MARSHALL, F. H. A. 1925. An Introduction to Sexual Physiology. *London* (Longmans, Green, and Co.).
- MAYR, E. 1939. The sex ratio in wild birds. *Amer. Nat.*, Vol. 73, pp. 156-179.
- MCCLEUNG, C. E. 1902. Notes on the accessory chromosome. *Anat. Anz.*, Bd. 20, pp. 220-226.
- McILHENNY, E. A. 1940. Sex ratio in wild birds. *The Auk*, Vol. 57, pp. 85-93.
- MOENKHAUS, W. J. 1911. The effects of inbreeding and selection on fertility, vigor, and sex ratio of *Drosophila ampelophila*. *Jour. Morph.*, Vol. 22, pp. 123-154.
- MOHR, O. L. 1923. A somatic mutation in the singed locus of the X chromosome in *Drosophila melanogaster*. *Hereditas*, Vol. 4, pp. 142-160.
- , and A. H. STURTEVANT. 1919. A semi-lethal in *Drosophila funebris* that causes an excess of males. *Proc. Soc. Exper. Biol. and Med.*, Vol. 16, pp. 95-96.
- MOORE, C. R. 1925. Sex determination and sex differentiation in birds and mammals. *Amer. Nat.*, Vol. 59, pp. 177-189.
- MORGAN, T. H. 1911. An alteration of the sex-ratio induced by hybridization. *Proc. Soc. Exper. Biol.*, Vol. 8, pp. 82-83.
- . 1912. The explanation of a new sex ratio in *Drosophila*. *Science*, Vol. 36, pp. 718-719.
- , C. B. BRIDGMAN, and A. H. STURTEVANT. 1925. The Genetics of *Drosophila*. *Bibl. Genet.*, Vol. 2, pp. 1-262.
- NIXON, J. W. 1916. War and national vital statistics with special reference to the Franco-Prussian War. *Jour. Roy. Stat. Soc.*, Vol. 79, pp. 418-444.
- NUMBAUM, M. 1897. Die Entstehung des Geschlechtes bei *Hydatina senta*. *Arch. f. Mikrosk. Anat.*, Bd. 49, p. 1897.
- ØKLAND, FRIDTJOF. 1932. Will It Be a Boy? New York (Century Co.).
- OPPENHEIM, F. 1926. Sex-ratio at birth of the Chinese. *China Med. Jour.*, Vol. 40, pp. 634-640.
- PARKER, G. H. 1914. A note on sex determination. *Science*, Vol. 39, pp. 215-216.
- PARKES, A. S. 1923. Studies on the sex ratio and related phenomena. 4. The frequencies of sex combinations in pig litters. *Biometrika*, Vol. 15, pp. 373-381.
- . 1924a. Studies on the sex-ratio and related phenomena. I. Foetal retrogression in mice. *Proc. Roy. Soc., Series B*, Vol. 95, pp. 551-558.
- . 1924b. Studies on the sex ratio and related phenomena. II. The influence of the age of the mother on the sex-ratio in man. *Jour. Genetics*, Vol. 14, pp. 39-47.

- . 1924c. Studies on the sex ratio and related phenomena. V. The sex ratio in mice and its variation. *Brit. Jour. Exper. Biol.*, Vol. 1, pp. 323-334.
- . 1926a. The mammalian sex-ratio. *Biol. Rev. and Biol. Proc. of the Cambridge Philos. Soc.*, Vol. 2, No. 1, pp. 1-51.
- . 1926b. Studies on the sex-ratio and related phenomena. (9). Observations on fertility and sex-ratio in mice, 1922-5. *Brit. Jour. Exper. Biol.*, Vol. 4, pp. 93-104.
- . 1926c. Studies on the sex-ratio and related phenomena. (8) The seasonal sex-ratio in the pig. *Zeitschr. f. indukt. Abstammungs- u. Vererbungsst.*, Bd. 40, pp. 121-138.
- , and J. C. DRUMMOND. 1925. The effect of vitamin B deficiency on reproduction. *Proc. Roy. Soc., Series B*, Vol. 98, pp. 147-171.
- , and —. 1926. The effects of fat-soluble vitamin A deficiency on reproduction in the rat. *Brit. Jour. Exper. Biol.*, Vol. 3, pp. 251-273.
- PEARL, M., and R. PEARL. 1908. On the relation of race crossing to the sex ratio. *Biol. Bull.*, Vol. 15, pp. 194-205.
- PEARL, R. 1916. Note on the proportions of the sexes in the whitefish. *Michigan Acad. of Science, Seventeenth Report*, p. 76.
- . 1917a. Report of progress on animal husbandry investigations in 1916. Part 3. The control of the sex ratio. *Maine Agric. Exper. Station Bull.*, No. 261, pp. 130-131.
- . 1917b. The sex ratio in the domestic fowl. *Proc. Amer. Philos. Soc.*, Vol. 56, pp. 416-436.
- . 1933. Statistical report on the fifth year's operations of the Bureau for Contraceptive Advice. *Fifth Rept. Bur. Contracept. Adv.*, Baltimore, pp. 5-17.
- . 1934. Constitutional factors in longevity. *Zeitschr. f. Morphol. u. Anthropol.*, Bd. 34, pp. 314-320.
- . 1936. Biological factors in fertility. *Annals Amer. Acad. Pol. and Soc. Sci.*, Vol. 188, pp. 14-25.
- . 1939. The Natural History of Population. *New York* (Oxford Univ. Press).
- , and H. M. PARSHLEY. 1913. Data on sex determination in cattle. *Biol. Bull.*, Vol. 24, pp. 205-225.
- , and R. N. SALAMAN. 1913. The relative time of fertilization of the ovum and the sex ratio amongst Jews. *Amer. Anthropol.*, Vol. 15, pp. 668-674.
- PINARD, A., and A. MAGNAN. 1913a. Sur la fragilité du sexe mâle. *C. r. des séances de l'Acad. des Sciences, Paris*, T. 156, pp. 401-403.
- , and —. 1913b. Recherches sur la sexualité dans les naissances. *C. r. des séances de l'Acad. des Sciences, Paris*, T. 156, pp. 1396-1399.
- PITT-RIVERS, G. H. L. F. 1927. The Clash of Culture and the Contact of the Races. *London*. (George Routledge and Sons).
- POWDERMAKER, HORTENSE. 1931. Vital statistics of New Ireland (Bismark Archipelago) as revealed by genealogies. *Human Biol.*, Vol. 3, pp. 351-375.
- POWYS, A. O. 1901. Data for the problem of evolution in man. *Anthropometric data from Australia. Biometrika*, Vol. 1, pp. 30-49.
- . 1905. Data for the problem of evolution in man. On fertility, duration of life and reproductive selection. *Biometrika*, Vol. 4, pp. 233-283.
- PRYLL, W. 1916. Kohabitationstermin und Kindsgeschlecht. *Münch. med. Wchnschr.*, Bd. 63, pp. 1579-1582.
- PUNNETT, R. C. 1904. On nutrition and sex determination in man. *Proc. Cambridge Philos. Soc.*, Vol. 12, Part IV, pp. 262-276.
- RAWLINGS, F. 1922. The interstitial gland and the sex problems. *Brit. Med. Jour.*, Vol. 2 for 1922, p. 29.
- RAWLS, ELIZABETH. 1913. Sex ratios in *Drosophila ampelophila*. *Biol. Bull.*, Vol. 24, pp. 115-124.
- REDFIELD, HELEN. 1926. The maternal influence of a sex-limited lethal effect in *Drosophila melanogaster*. *Genetics*, Vol. 11, pp. 482-502.
- REED, T. E. 1913. Sex, Its Origin and Determination. *New York* (Rebman Co.).
- RIDDLE, O. 1925. Sex in a fraternity of pigeons obtained from an interfamilial cross. *Anat. Rec.*, Vol. 31, pp. 349-350.
- . 1927. Some aspects of sexual difference in prenatal growth and death. *Amer. Nat.*, Vol. 61, pp. 97-112.
- . 1932. Metabolism and sex. In *Sex and Internal Secretions*, Edited by Edgar Allen. *Baltimore* (Williams & Wilkins). Pp. 246-280.
- RUSSELL, W. T. 1936. Statistical study of the sex-ratio at birth. *Jour. Hyg.*, Vol. 36, pp. 381-401.
- SADLER, M. T. 1830. The Law of Population. *London* (John Murray).
- SAVORGAN, F. 1921. L'aumento delle nascite maschili durante la guerra. *Metron*, Vol. 1, pp. 131-160.
- . 1933. La Statistica delle Nascite Legittime secondo l'Ordine di Generazione. Movimento della Popolazione secondo gli Atti dello Stato Civile negli Anni 1929 e 1930. *Roma* (Istituto Poligrafico dello Stato).
- SCHENK, L. 1902. Meine Methode der Geschlechts-

- bestimmung. *Verhandl. d. V. Internat. Zool.-Congresses zu Berlin*, pp. 363-402.
- SCHNEIDER, B. A. 1940. Thyroid feeding and metamorphosis. I. The influence of various concentrations of thyroid substance on metamorphosis and growth of the flour beetle, *Tribolium confusum* Duval. *Jour. Exper. Zool.*, Vol. 84, pp. 113-139.
- SCHOTT, R. G., and W. V. LAMBERT. 1930. The normal variability of the sex-ratio in the guinea pig. *Iowa State Coll. Jour. of Science*, Vol. 4, pp. 343-349.
- SCHULTZ, A. H. 1918. Studies in the sex-ratio in man. *Biol. Bull.*, Vol. 34, pp. 257-275.
- . 1921. Sex incidence in abortions. *Carnegie Inst. of Washington Publ.* 275. *Contrib. to Embryol.*, No. 36, Vol. 12, pp. 177-191.
- SCHULTZE, O. 1904. Zur Frage von den geschlechtbildenden Ursachen. *Arch. f. Mikrosk. Anat.*, Bd. 63, pp. 197-257.
- SILJOGREN, E. 1895. Zur Bestimmung und Entstehung des Geschlechts. *Centralbl. f. Gynäk.*, Bd. 19, pp. 590-595.
- SHAFTESBURY, A. D. 1934. The Siphonaptera (fleas) of North Carolina, with special reference to sex ratios. *Jour. Elisha Mitchell Scientif. Soc.*, Vol. 49, pp. 247-263.
- SHULL, A. F. 1925. Sex and the parthenogenetic-bisexual cycle. *Amer. Nat.*, Vol. 59, pp. 138-154.
- SIMONE, P. W. 1916. Zur willkürlichen Geschlechtsbestimmung. *Münch. med. Wchnschr.*, Bd. 63, pp. 1783-1788.
- . 1917. Gewollte und ungewollte Schwankungen der weiblichen Fruchtbarkeit. Bedeutung des Kohabitationstermines für die Häufigkeit der Knabengeburten. *Berlin* (Julius Springer).
- SIMMOTT, E. W., and L. C. DUNN. 1939. Principles of Genetics. New York (McGraw-Hill Book Co.).
- SLOANER, J. R. 1939. The effect of different percentages of protein in the diet of six generations of rats. *Stanford Univ. Publ., University Series, Biol. Sciences*, Vol. 6, No. 4.
- , and T. A. CARD. 1913. The effect of a restricted diet. V. On mortality, cannibalism and the sex ratio. *Amer. Jour. Physiol.*, Vol. 64, pp. 297-310.
- SWENBY, A. 1916. Über die Geburt bei Minderjährigen. *Zentralbl. f. Gynäk.*, Bd. 40, pp. 60-74.
- SZADINKO, O. 1908. Das Geschlechtsverhältnis bei den Geburten in Oesterreich. *Arch. f. Gynäk.*, Bd. 84, pp. 741-824.
- STIEDA, W. 1875. Das Sexualverhältnis der Geborenen. *Statist. Mittell., Strassburg*, Heft 3.
- STURTEVANT, A. H., and G. W. BEADLE. 1939. An Introduction to Genetics. Philadelphia and London (W. B. Saunders Co.).
- SUMNER, F. B., M. E. McDANIEL, and R. R. HUMPHRIS. 1922. A study of influences which may affect the sex-ratio of the deer-mouse (*Peromyscus*). *Biol. Bull.*, Vol. 43, pp. 123-165.
- TAUBIG, F. J. 1936. Abortion, Spontaneous and Induced. St. Louis (C. V. Mosby).
- TEURY, M. 1864. Ueber das Gesetz der Erzeugung der Geschlechter bei den Pflanzen, den Thieren und dem Menschen. *Leipzig*.
- VIGOR, H. D., and G. U. YULE. 1906. On the sex ratios of births in the registration districts of England and Wales. *Jour. Roy. Statist. Soc.*, Vol. 69, pp. 576-582.
- WADDINGTON, C. H. 1939. An Introduction to Modern Genetics. New York (Macmillan Co.).
- WALL, A. J. 1887. Some considerations in regard to the causation of sex. *Lancet*, Vol. 1 for 1887, pp. 261-263; 307-309.
- WARREN, D. C. 1918. The effect of selection upon the sex-ratio in *Drosophila ampelophila*. *Biol. Bull.*, Vol. 34, pp. 351-371.
- WELDON, W. F. R. 1906. On heredity in mice from the records of the late W. F. R. Weldon. Part I. On the inheritance of the sex-ratio and of the size of litter. *Biometrika*, Vol. 5, pp. 436-449.
- WENTWORTH, E. N. 1914. Sex in multiple births. *Science*, Vol. 39, p. 611.
- WHITNEY, L. F. 1939. The sex ratio in dogs maintained under similar conditions. *Jour. Hered.*, Vol. 30, pp. 388-389.
- WILCKENS, M. 1886. Untersuchung über das Geschlechtsverhältnis und die Ursachen der Geschlechtsbildung bei Haustieren. *Biol. Centralbl.*, Bd. 6, pp. 503-510.
- WILLIAMS, B. H. 1939. The embryonic development of sex. In *Sex and Internal Secretions*, Second Edition, Edited by Edgar Allen, C. H. Danforth, and E. A. Doisy. Baltimore (Williams & Wilkins). Pp. 64-144.
- WILLOUGHBY, R. 1931. The families of freshmen. *Human Biol.*, Vol. 3, pp. 342-350.
- WINSTON, S. 1932. Some factors related to differential sex-ratios at birth. *Human Biol.*, Vol. 4, pp. 272-279.
- WITTECH, E. 1929. Studies on sex differentiation and sex determination in amphibians. III. Rudimentary hermaphroditism and Y chromosome in *Rana temporaria*. *Jour. Exper. Zool.*, Vol. 54, pp. 157-223.

- . 1934. Genes and inductors of sex differentiation in amphibians. *Biol. Rev.*, Vol. 9, pp. 460-488.
- WOLLA, G. 1927. Akklimatisierung und Deklimatisierung. II. Analyse der holländischen Geburtsperiodizität auf Grund ornithologischer Untersuchungen. *Genetica*, Vol. 9, pp. 157-216.
- WOODS, F. A. 1906. The non-inheritance of sex in man. *Biometrika*, Vol. 5, pp. 73-78.
- WYLLIE, J. 1933. Sex differences in infant mortality. *Canadian Publ. Health Jour.*, March, pp. 177-185.
- YERUSHALMY, J. 1939. Age of father and survival of offspring. *Human Biol.*, Vol. 11, pp. 342-356.





CHEMICAL STRUCTURE OF THE RED BLOOD CELL

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THE highly differentiated, specific structure of the red blood cell is adapted to its main physiologic rôle. As Ponder (1934) has shown, the peculiar, biconcave shape of the erythrocyte appears to be most opportune from the standpoint of diffusion. It is a compromise between a sphere, which would offer the greatest carrying capacity with the smallest amount of structural material, and an infinitely thin disc, which would present the most favorable conditions for diffusion.

It would appear, therefore, that enclosure of the respiratory pigment in the peculiarly formed structure of the red blood cell allows the hemoglobin to function most efficiently. In addition, the striking differential permeability to ions which distinguishes the erythrocyte is an essential feature in the maintenance of a constant blood reaction. As so aptly stated by Barcroft (1921): "In the interior of the red blood corpuscle the hemoglobin exists in a world of its own; by this device nature has at a stroke increased the efficiency both of the blood and of the hemoglobin."

Since the time of Leeuwenhoek (1719) the actual structure of the mammalian erythrocyte has been a debatable question. His view held that the hemoglobin sol is surrounded by a membrane which gives rise to the so-called "ghosts" after hemolysis (Jorpes, 1932). Rollett (1870)

introduced the term stroma to designate the sponge-like network, in the meshes of which he believed the hemoglobin solution to be held. The predominant view at present accepts the erythrocyte as a balloon-like structure, consisting of a semipermeable cell membrane or envelop of complex mosaic type enclosing hemoglobin, salts, and other substances in solution. The presence of a fine stroma network or a fluid cytoplasm capable of gelation under certain circumstances, is still speculative. However, as Ponder (1936) has stated, "The idea that the mammalian red cell is a bag filled with salts, pigment, and water, inert and dead or dying, is quite wrong, for it has a measurable metabolism of a rather complicated kind which is smaller than, but otherwise similar to, that of more fully organized cells."

SIMULTANEOUS COORDINATED STUDIES

When compared to the thoroughness with which hemoglobin has been investigated, our chemical understanding of the structural elements of the mammalian red corpuscle is surprisingly meager and inadequate. A thorough investigation of the structural elements of the red blood cell is complicated by the small amounts of this material which are so intimately combined with far greater quantities of hemoglobin (less than 10 per cent of the total solids of the whole cell is stroma;

up to 95 per cent is hemoglobin). Difficulties are encountered in separating, without appreciable loss or change in chemical composition, the framework of the cells from the associated hemoglobin and from contaminants; also in applying micromethods of sufficient scope and accuracy to permit differential studies of both the intact cells and stroma from a single sample of blood. This paper is a review of the results so far obtained from the coordinated studies which constitute the blood chemistry program of the Research Laboratory of the Children's Fund of Michigan; a program involving the cooperative efforts of numerous investigators and designed to obtain information about the chemical structure of the red blood cell. These integrated studies, covering a period of seven years and embracing observations on the physical and chemical characteristics of the blood in the normal individual (Erickson, Williams, Hummel and Macy, 1937a), in pathologic states (Erickson, Williams, Hummel, Lee and Macy, 1937b; Williams, Erickson, Bernstein, Hummel and Macy, 1937), and from investigation of practically hemoglobin-free posthemolytic residues prepared from various species (Beach, Erickson, Bernstein, Williams and Macy, 1939; Bernstein, Jones, Erickson, Williams, Avrin and Macy, 1938; Erickson, Williams, Bernstein, Avrin, Jones and Macy, 1938; Williams, Erickson, Avrin, Bernstein and Macy, 1938), have contributed pertinent information on the chemical nature of the red blood cell framework and serve as the basis for the discussion in the following pages.

An outline of the program is shown in Figure 1. This chart pictures the correlated physical measurements and chemical determinations utilized and emphasizes the importance of simultaneous observations on the same blood samples,

as requirement for more complete understanding of the chemical structure of the erythrocyte.

The red cell in anemias

The various hemolytic and hypochromic anemias of the child and the hypochromic and pernicious anemias of the adult demonstrate extreme abnormalities in shape, size, weight and fragility of the erythrocyte which are characteristic of each type of anemia. A study of the chemical composition of the erythrocytes in these blood dyscrasias has pointed to the marked alterations which occur in their structural framework.

An outstanding change found in the anemic cell is the elevated cation content, a reflection of the increased sodium and potassium concentrations. The anion content of the corpuscles is usually found to be lower than normal. Maizels (1936) showed that the amount of base present in the normal erythrocyte is greater than that required to combine with cell chloride, bicarbonate, and hemoglobin. He suggested that the excess cations, found to range between 7 and 20 milliequivalents (meq.) per liter of cells, were in combination with some unknown anion (X^-) present in the corpuscle. Recently, Farmer and Maizels (1939) have shown that a part of the anion (X^-) is acid-soluble phosphates and glutathione.

A definite parallelism seems to exist between the excess corpuscular base and the undetermined weight of the cell calculated by subtracting the sum of the weights of corpuscular hemoglobin, water, total ions, and total lipids from the corpuscular weight. This undetermined weight probably consists chiefly of the structural protein, in addition to other substances such as non-protein nitrogen compounds, phosphoric esters, etc.

**INTEGRATED BLOOD PROGRAM
RESEARCH LABORATORY
CHILDREN'S FUND OF MICHIGAN
(1931-1939)**

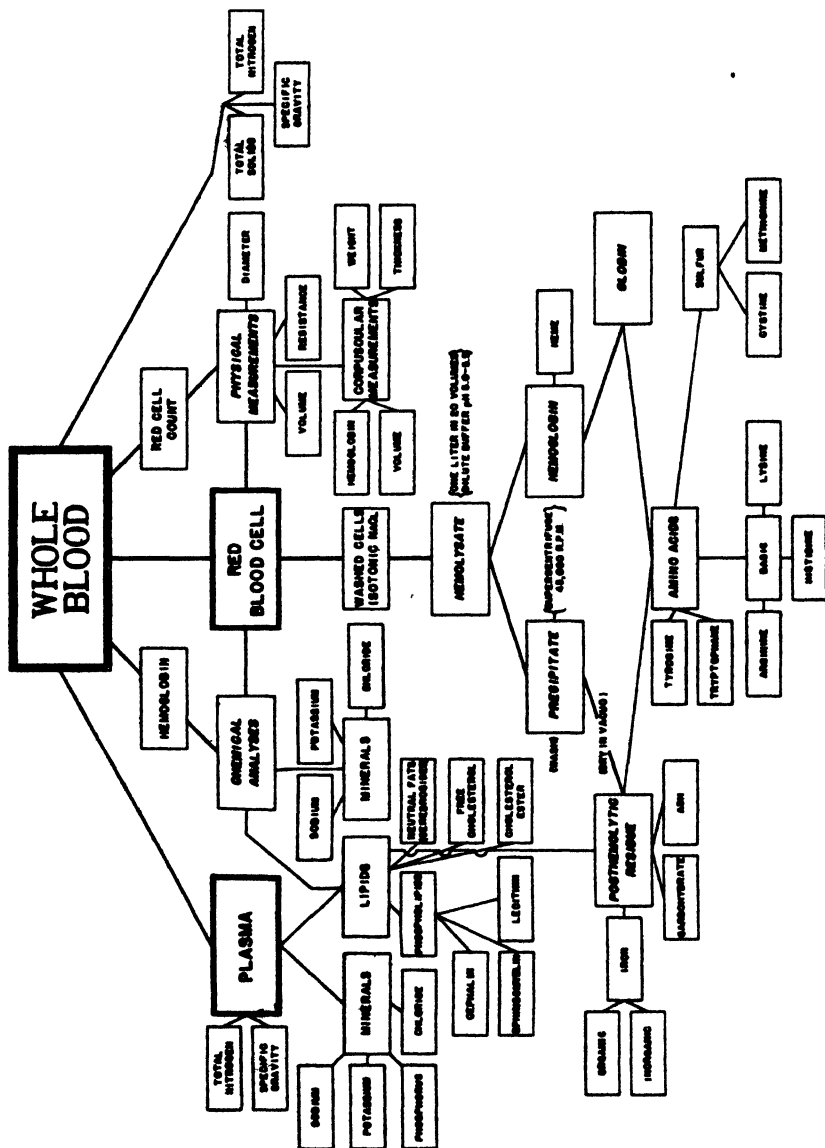


FIG. 1

The premise has been accepted that, in contrast to the plasma, the lipid composition of the erythrocyte remains relatively unchanged under a variety of conditions. In harmony with this accepted view the lipid composition of the red blood cells of normal children has been demonstrated to be not only relatively constant in amount and distribution, but similar in composition to the erythrocyte in adults. However, it has been found that, just as in plasma, certain definite changes occur in the red cell in the various types of anemia. Normally the various lipid constituents which make up the total lipid content of the red cell maintain a characteristic pattern, that is, approximately 58 per cent of the total is phospholipid, 23 per cent free cholesterol, 12 per cent neutral fat and 7 per cent cholesterol esters. Recently, seventy-five per cent of the neutral fat has been shown to be cerebrosides (Erickson, Souders, Shepherd, Teague and Williams, 1940). The outstanding changes in anemia are a lowered concentration in corpuscular phospholipid and a marked increase in cholesterol esters.

The physical and chemical abnormalities which the corpuscle exhibits in anemia are the result of a pathological process and may produce an impairment of the physiological activity or efficiency of the erythrocyte. On the other hand, it would not be unexpected to find the individual corpuscle more active because of the increased demands placed upon the reduced numbers to carry on the normal biochemical functions.

Bloor and his school (Bloor, Okey and Corner, 1930; Bloor and Snider, 1934; Boyd, 1935) have demonstrated that greater physiological activity in a tissue or organ is associated with increased amounts of phospholipid and free cholesterol; lowered physiological activity, de-

generation, and retrogression are accompanied by decreased quantities of these particular lipids and augmented amounts of neutral fat and cholesterol esters. In this connection Gerard (1912) has suggested that higher potassium to sodium ratios in tissues are related to a higher state of activity. Also, it must be remembered that the term physiological activity (Bloor, Okey and Corner, 1930) is not confined to respiratory exchange but is meant to include all the physiologic processes of the living cell. Not only is the phospholipid decreased and the cholesterol esters increased in the anemic erythrocyte, but the potassium to sodium ratio is lower than in the normal.

If one accepts, therefore, the current views with regard to physiological activity, the lipid and mineral composition of the abnormal erythrocytes in the hereditary anemias of childhood and in pernicious anemia indicates that the cells are not only in a state of lowered function or activity, but also in a state of degeneration and retrogression. These results emphasize the view that the erythrocyte is an organized vital entity and not a hemoglobinized cellular corpse and that it experiences reactions such as lowered physiological activity, retrogression and degeneration similar to those of the more highly organized tissue cells in pathological conditions.

CHEMICAL COMPOSITION OF "POSTHEMOLYTIC RESIDUE"

Knowledge concerning the chemical nature of the structure of the erythrocyte has stimulated postulations involving both lipids and proteins. The importance of the lipids and minerals have been emphasized from the evidence secured through studies of the red blood corpuscle in the various types of anemia. Chemical studies on the protein phase of the cell

framework, however, necessitate isolation of the structural material from the hemoglobin which comprises 90 to 95 per cent of the total red blood cell solids.

Methods for isolating the insoluble part of the erythrocyte which remains after hemolysis have been proposed by several investigators. A variety of terms such as red blood cell membrane, shadows, ghosts, or stroma have been suggested. It would seem preferable, however, until it can be determined whether the cell shadows or ghosts represent a membrane, an internal network or stroma, or a combination of both, that the material be designated by the term "posthemolytic residue".

Previous methods which have been proposed for the preparation of the posthemolytic residue have yielded products high in hemoglobin, and of altered composition due to the use of lipid solvents. After study and comparison of the former procedures, a method was finally developed in this Laboratory which yielded posthemolytic residues of consistent composition for similar samples of red blood cells and with comparatively little hemoglobin contamination.

Posthemolytic residues were prepared from the red cells of a number of species. Elementary analyses of these preparations are given in Table 1. The average hemoglobin content in all preparations was found to be 10 per cent or less, with the exception of the human residues. It can be seen that the posthemolytic residue is mainly a mixture of protein and lipid. The importance of this protein-lipid complex is shown by the fact that continuous extraction in a Soxhlet apparatus is required to liberate the lipids. Furthermore, vigorous washing procedures do not disturb the combination as the same sample followed through as many as five consecutive washings remained unaltered

in composition. This demonstrated, also, that the lipids of the red blood cells are bound in the framework of the erythrocyte, for no significant amounts could be recovered from either the hemolysate or wash solutions. The latter is important, as analysis of the lipids permits a limited study of structural changes in the erythrocyte under various conditions without actual posthemolytic residue preparation.

Among the five mammalian species, beef, sheep, and horse posthemolytic residues are high in protein content and

TABLE 1
Composition and lipid distribution of posthemolytic residues from various species

	BEEF	SHEEP	HORSE	HUMAN	AVIAN
	(per cent of total residue)				
Hemoglobin.....	5	2	10	23	5
Ash.....	3	3	2	5	2
Protein.....	57	68	53	50	89
Lipid.....	26	24	20	11	4
	(per cent of total lipid)				
Phospholipid.....	62	62	63	65	83
Free cholesterol.....	27	20	34	20	14
Cholesterol esters.....	3	0	2	4	0
Neutral fat.....	8	18	1	11	3
Protein:lipid ratio.....	2	3	3	5	22

human is low (Table 1). The result is a low protein to lipid ratio for the first three species and approximately twice this for the human preparations. The nucleated avian red cell residues contain a comparatively small amount of lipid material and as a result the ratio of protein to lipid is quite high.

Inasmuch as the residues from the various species demonstrate differences in lipid concentration, it is interesting to compare their concentrations to the lipid content and physical characteristics of the erythrocytes of the individual species

(Table 2). The lipid concentration per 100 grams of cells in the various species appears unrelated to the residue composition. The sheep cells have the highest concentration on the unit weight basis and the beef cells the lowest.

The erythrocytes of the various species, however, differ in their hematological and physical characteristics, cell hemoglobin content, volume, weight, and diameter. The red cells of sheep and

TABLE 2

Hematological and physical measurements of erythrocytes of different species

	BEEF	SHEEP	HUMAN	AVIAN
Red blood cells (millions per c.mm.).....	8.4	10.7	5.2	3.0
Hemoglobin:				
Grams per 100 cc. . .	13.4	—	14.0	10.3
Per cell (micromicrograms).....	16.3	11.0	29.0	34.4
Corpuscular measurements:				
Volume (cu)	56.5	37.7	86.0	117.6
Weight (micromicrograms).....	61.1	40.8	93.0	129.7
Diameter (μ).....	5.9	5.3	7.7	12.1
Thickness (μ).....	2.1	1.9	1.8	1.0
Diameter:thickness ratio.	2.8	2.8	4.1	12.1
Total lipid (mg. per 100 gm.).....	375	595	424	550
Total corpuscular lipids (mg. $\times 10^{-12}$ per cell)...	222	243	394	716

beef are small, weighing approximately 41 and 61 micromicrograms, respectively, as compared to human and avian cells which weigh 93 and 130 micromicrograms, respectively. Because 100 grams of sheep cells contain approximately 2 to 3 times as many erythrocytes as the same weight of human and avian cells, analyses expressed on a unit weight basis obscure significant differences in composition of the various species' erythrocytes. When the lipid composition of

the average single corpuscle of each species is calculated it is significant to see the order in which they are related. The beef and sheep red corpuscles, which show the highest concentration of lipids in the posthemolytic residue and are the smallest cells, have the lowest concentration of corpuscular lipid. On the other hand, the avian corpuscles, with the highest lipid concentration and largest dimensions, give a residue of very low lipid content. The human cells and residues are intermediate in their dimensions and lipid content. In the species studied, there appears to be an inverse relationship between the lipid content of the residue or framework of the cell and the corpuscular lipid concentration. It is now evident that the structural part of the red blood cell is a complex compound of, in the main, protein and lipid. What are the characteristics of these two phases from the standpoint of chemical makeup?

Lipids in "posthemolytic residues"

Table 1 also presents the results of differential lipid analyses of the posthemolytic residues of the various species. Phospholipid and free cholesterol make up the major portion of the total lipid. The mammalian residues are quite comparable in their phospholipid makeup, which comprises a little over 60 per cent of the total lipid. Avian residue is much higher in phospholipid with a concomitant decrease in the other fractions. The lipid distribution of these residues is quite similar to that of the corresponding erythrocytes.

Recently, with the aid of newly developed methods, we have demonstrated that cephalin is normally the major component of the phospholipids of the red blood cell and posthemolytic residue. The remaining portion is divided about

equally between lecithin and sphingomyelin. Furthermore, the lipid constituent of the erythrocyte and residue which has been called neutral fat appears to consist largely of cerebrosides. Inasmuch as cephalin, which is found to be the predominant cellular phospholipid, is considered to be the structural type of phospholipid whereas lecithin is designated as the metabolic type (Sinclair, 1934), these observations are additional evidence to that previously given, that the lipids of the red cell are, normally, bound in the framework.

The fact that phospholipid and free cholesterol comprise practically all of the total lipid of the posthemolytic residue not only identifies this substance as protoplasmic in nature but supports the view that the red cell is a living entity. The French school of workers, Mayer, Schaeffer and Terroine, have demonstrated, and Bloor and his school, in this country, have confirmed the essential rôle that phospholipids and cholesterol play in the vital economy of living cells (Bloor, 1928; Bloor, Okey and Corner, 1930). These particular lipids are found to be present in constant amounts in living tissue irrespective of the state of nutrition. They are designated as the *element constant* and considered to be constant and integral components of protoplasm.

Protein in "posthemolytic residues"

The next consideration is the protein moiety which makes up two-thirds to three-fourths of the structural entity of the red cell. Seven amino acids have been determined in the lipid extracted posthemolytic residues of five different species and results of these analyses are shown in Table 3. It is evident that the residue proteins of the various species are similar with respect to the content of amino acids here determined. The cystine and

methionine contents account for 85 to 95 per cent of the total sulphur and show the greatest variations among the different species. The values for histidine, arginine, tyrosine and tryptophane are slightly lower, but otherwise similar to the values obtained by Jorpes on his preparations. The seven amino acids thus far determined account for 25 to 27 per cent of the total protein nitrogen.

TABLE 3

Nitrogen of amino acids expressed as per cent of total nitrogen of the posthemolytic residue

	BEEF	SHEEP	HORSE	HOG	HUMAN
Histidine.....	4.0	4.7	4.2	4.5	4.3
Arginine.....	12.0	11.4	11.6	11.4	11.8
Lysine.....	4.8	4.5	5.4	5.1	5.8
Tyrosine.....	1.6	1.4	1.6	1.6	1.7
Tryptophane.....	1.2	1.0	1.1	1.3	1.2
Cystine.....	0.7	0.8	0.8	1.0	0.8
Methionine.....	1.2	1.6	1.6	1.5	1.4
Per cent nitrogen accounted for....	25.5	25.4	26.3	26.4	27.0

TABLE 4

Per cent average basic amino acid composition of lipid-extracted posthemolytic residue, compared with values in the literature for serum orosin, hemoglobin and cattle fibrin

	HISTIDINE	ARGININE	LYSINE
Posthemolytic residue....	2.1	5.0	3.6
Serum orosin.....	2.1	4.7	6.9
Hemoglobin.....	7.5	3.3	7.9
Cattle fibrin.....	2.5	7.7	10.1

On the basis of these determinations the proteins of the various residues appear to be quite similar. The content of basic amino acids indicates that the protein moiety of the red cell framework is acidic in nature as stated by Jorpes (1932). Table 4 presents a comparison of the basic amino acid composition of the posthemolytic residue protein and other blood

proteins. The distribution of the basic amino acids in the posthemolytic residue preparations is obviously different from that of hemoglobin and fibrin. It is similar in composition to Block's serum orosin with respect to histidine and arginine. The serum orosin, however, contains approximately twice as much lysine as the posthemolytic residue protein. Not only are the proteins of the posthemolytic residues different in composition from the other known blood proteins but they are also characteristic substances themselves. While at present there is no assurance that the protein moiety of the erythrocyte residue is composed of a single protein, it seems certain that if there are two or more individual proteins present, they appear in the erythrocyte framework of all these various species in the same proportions.

Erythrocytes in a controlled anemia

Finally, in an effort to study directly the effect of a pathological condition on the chemical composition of the erythrocyte framework, posthemolytic residue was prepared from red cells in an experimental anemia which is known to affect the hematological (Gruhzit, 1931), physical and chemical characteristics of the corpuscle (Williams, Erickson, Black and Macy, 1941). Dogs were maintained in a moderate to severe state of anemia with normal propyl disulphide for a period of three months. At the end of this time they were exsanguinated and posthemolytic residue was prepared from the combined washed erythrocytes of the animals. Another residue preparation was made from the blood of normal dogs.

Fractional lipid and protein analyses of the anemic dog blood material showed a content of 71 per cent protein and 12 per cent lipid, making the protein:lipid ratio 5.9. In the normal dog blood material

the protein constituted 57 per cent, the lipid 17 per cent, a protein:lipid ratio of 3.4 (unpublished data). It can be seen that the protein to lipid ratio was increased by the anemia. This is significant in the light of the changed dimensions of the erythrocytes as the result of the anemia. The anemic erythrocytes were larger and heavier, more like the pernicious anemia red cell. In addition, the total base of the cell was augmented, indicating an increase in the anion (X^-) similar to that found in the human anemias had occurred.

The quantity of red cell framework

The question may be asked: How much of the cell is taken up by the fixed framework? No attempt has been made to secure a quantitative yield of residue from the red cells, as it was essential to reduce the hemoglobin content of the product to a minimum with vigorous washing procedures. It is possible, however, to calculate the quantity of fixed framework, if we assume that all of the cell phospholipid is bound as such. Evidence has been given that such an assumption is relatively safe with respect to the normal erythrocyte.

Table 5 shows how this calculation may be made. The results of the calculation of the per cent of structural material of the red blood cell of various species are presented together with the values obtained for rabbit erythrocytes by Fricke, Parker and Ponder (1939) using the conductivity method. The erythrocytes of the various mammalian species have from 1 to 4 per cent structural material. The large nucleated avian cell has a much larger amount, 13 per cent. The amount of structural material is relatively increased in the anemic cell and may be related to a number of factors. It will be recalled that the residue protein is acidic in nature and that in the anemias

the elevated base tends to parallel the undetermined cell weight.

TABLE 5

Calculation of fixed framework of erythrocytes of various species

Weight of phospholipid per average cell
 Per cent phospholipid in residue
 = Weight of residue per average cell
 Weight of residue
 Weight of average cell $\times 100$ = Per cent of fixed framework in an average red blood cell

	PER CENT
*Rabbit.....	2.3
Beef.....	1.3
Sheep.....	2.3
Human.....	3.3
Avian.....	13.3
Dog(normal).....	4.2
Dog(anemic).....	6.7

* From Fricke, Parker, and Ponder. 1939.

SUMMARY

It appears, from the evidence at hand, that the red blood cell is a definitely organized complex. The hemoglobin and salts are held in a composite structure, the essential components of which are protein and lipid. The different hematological and physical characteristics of the erythrocytes obtained from various species seem to be associated with the quantity relationship of the protein-lipid complex of the red cell framework. The fact that the protein and lipid patterns are remarkably similar in the different species and that in certain pathological states the lipid pattern, at least, undergoes marked alteration points to the red blood cell as a vital entity similar to other tissue cells which likewise undergo chemical changes under pathological circumstances.

LIST OF LITERATURE

- BARCROFT, JOSEPH. 1921. The Raison d'Etre of the Red Corpuscle. *The Harvey Lectures*, Ser. XVII: 146-163, Philadelphia.
- BEACH, ELIOT F., ERICKSON, BETTY N., BERNSTEIN, SAMUEL S., WILLIAMS, HAROLD H., and MACY, ICIE G. 1939. The amino acid composition of erythrocyte posthemolytic residue of five mammalian species. *J. Biol. Chem.*, 128: 339-346.
- BERNSTEIN, SAMUEL S., JONES, ROBERT L., ERICKSON, BETTY N., WILLIAMS, HAROLD H., AVRIN, IRA, and MACY, ICIE G. 1938. A method for the preparation of posthemolytic residue or stroma of erythrocytes. *J. Biol. Chem.*, 122: 507-514.
- BLOOR, W. R. 1928. Distribution of unsaturated fatty acids in tissues. III. Vital organs of beef. *J. Biol. Chem.*, 80: 443-454.
- , OKEY, RUTH, and CORNER, GEORGE W. 1930. The relation of the lipids to physiological activity. I. The changes in the lipid content of the corpus luteum of the sow. *J. Biol. Chem.*, 86: 291-306.
- , and SNIDER, RUTH H. 1934. Phospholipid content and activity in muscle. *J. Biol. Chem.*, 107: 459-470.
- BOYD, ELDON M. 1935. The lipid content of the Jelly of Wharton. *J. Biol. Chem.*, 111: 667-669.
- ERICKSON, BETTY N., SOUDERS, HELEN J., TEAGUE, D. MAXWELL, and WILLIAMS, HAROLD H. 1940. Relation between cerebroside and neutral fat contents of blood plasma, erythrocytes and stroma. *Proc. Soc. Exper. Biol. and Med.*, 45: 153-156.
- ERICKSON, BETTY N., WILLIAMS, HAROLD H., HUMMEL, FRANCES C., and MACY, ICIE G. 1937a. The lipid and mineral distribution in the serum and erythrocytes of normal children. *J. Biol. Chem.*, 118: 15-35.
- , —, —, LEE, PEARL, and MACY, ICIE G. 1937b. The lipid and mineral distribution of the serum and erythrocytes in the hemolytic and hypochromic anemias of childhood. *J. Biol. Chem.*, 118: 569-598.
- , —, BERNSTEIN, SAMUEL S., AVRIN, IRA, JONES, ROBERT L., and MACY, ICIE G. 1938. The lipid distribution of posthemolytic residue or stroma of erythrocytes. *J. Biol. Chem.*, 122: 515-528.
- FARMER, STANLEY N., and MAIZELS, MONTAGUE. 1939. Organic anions of human erythrocytes. *Biochem. J.*, 33: 280-289.
- FRICKE, HUGO, PARKER, EDW., and PONDER, ERIC. 1939. Relative quantity of the fixed framework

- of the hemolyzed rabbit red cell. *J. Cell. and Comp. Physiol.*, 13: 69-76.
- GERARD, P. 1912. Teneur en potassium et en sodium des différents organes d'un chien. *Comp. rend. Acad.*, 154: 839. Cited in: PETERS, J. P., and VAN SLYKE, D. D. 1931. Quantitative Clinical Chemistry, Vol. I, Interpretations, p. 754. Williams & Wilkins Co., Baltimore.
- GRAUZEIT, O. M. 1931. II. Anemia in dogs produced by feeding disulphide compounds. *Am. J. Med. Sciences*, 181: 815-820.
- JORPES, ERIK. 1932. The protein component of the erythrocyte membrane or stroma. *Biochem. J.*, 26: 1488-1503.
- MAIZELS, MONTAGUE. 1936. The anion and cation contents of normal and anaemic bloods. *Biochem. J.*, 30: 821-830.
- PONDER, ERIC. 1934. The Mammalian Red Cell and the Properties of Haemolytic Systems. (Verlag von Gebrüder Borntraeger), Berlin.
- PONDER, ERIC. 1936. The kinetics of hemolysis. *Physiol. Reviews*, 16: 19-51.
- ROLLETT, A. 1870. In: Manual of Human and Comparative Histology. Edited by S. Stricker, p. 408. The New Sydenham Society, London.
- SINCLAIR, R. G. 1934. The physiology of the phospholipids. *Physiol. Reviews*, 14: 351-403.
- WILLIAMS, HAROLD H., ERICKSON, BETTY N., BERNSTEIN, SAMUEL S., HUMMEL, FRANCES C., and MACY, ICIE G. 1937. The lipid and mineral distribution of the serum and erythrocytes in pernicious anemia. Before and after therapy. *J. Biol. Chem.*, 118: 599-618.
- , —, AVERIN, IRA, BERNSTEIN, SAMUEL S., and MACY, ICIE G. 1938. Determination of cephalin in phospholipids by the estimation of choline. *J. Biol. Chem.*, 123: 111-118.
- , —, BRACH, ELIJOT F., and MACY, ICIE G. 1941. Biochemical studies of the blood of dogs with *n*-propyl disulfide anemia. *J. Lab. and Clin. Med.* In Press.





PULSE RATES

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WHEN the *Medical Impairment Study* of 1929 (1) was in course of preparation, during 1931, it seemed desirable to preface the investigation of abnormal pulse by a review of some of the characteristics of normal pulse. As both time and space were limited, the matter was summarized in a brief reference to the average pulse rates for men (74.7) and women (75.8), derived from 30,000 insured lives resident in the United States and Canada. It may be of interest to review here at this time some of the other matters dealing with pulse rates, which were brought together in connection with this medical research.

The pulse rate in human beings was observed three or four centuries before the Christian era, but not until Harvey, in 1614, discovered the fact that the blood circulates through the body, was there any incentive to record the rate at which the heart does its pumping. Early in the following century the pulse watch was invented, but for another hundred years little of permanent value was recorded scientifically regarding pulse rates.

Upon surveying the literature of the subject—and definite facts were not easily accessible—it appears that the classic paper was that of Dr. William A. Guy (19). His observations were made on healthy men who had not eaten food for

two hours previously; they were made between noon and 2 P.M. before any violent exercise or excitement. The pulse was taken first in the erect, then in the sitting and then in the recumbent posture. In the sitting posture the back was unsupported; in the recumbent position the head was slightly raised. A short interval was allowed to elapse after each change in posture. One hundred such cases were examined, aged from 20 to 50 and averaging 27 years. The extreme cases were found to differ considerably from the mean readings; thus between standing and lying the difference ranged from 44 to 4 pulsations per minute. Two general rules were deduced,—first, a change from the erect to the sitting, from the sitting to the recumbent or from the erect to the recumbent position, lessens the frequency of the pulse; second, the difference between pulse when standing and sitting is greater than between sitting and lying. After all exceptions to these rules had been excluded, there were 66 experiments which gave the following average readings for men at mean age 27:—

standing 81.0; sitting 71.1; lying 65.6.

Similar procedure for 50 women gave the following readings:—

standing 91.3; sitting 84.4; lying 79.7.

Dr. Guy stated his belief that muscular contraction, whether employed to change

the position of the body or to maintain it in the same position, accelerates the pulse. He showed that taking a meal may normally increase the pulse rate of a healthy person by from ten to twenty beats per minute; and that the pulse rate in the evening differs from that of the morning by about the same amount.

For many years the textbooks and encyclopedias have given 72 as the average pulse rate per minute for men, and 80 for women. This results in an excess of eight per minute for women as contrasted with only one per minute in the 30,000 lives referred to above. It has been suggested that the relatively lower pulse rates for women today may be due to (1) the more athletic, out-door life of modern times and (2) absence of the nervousness which was doubtless often present on examination a century ago.

Mary Hallock (23) has contributed an interesting discussion on pulse and rhythm. The close connection between pulse and rhythm has been speculated upon since the fourth century B.C.—it will be recalled that the circulation of the blood was not discovered until shortly before Shakespeare's death. Seventeen bandmasters have reported a "beat" of 64 to 72 per minute; this was what soldiers had found it agreeable to march to. On the other hand, it has been noted that the favorite metronome of the composer Chopin was 88 per minute. He was of a nervous, tubercular nature and his own pulse rate was probably not far different from this figure. "Perhaps the arm of knowledge can thus measure the living pulse of those who have long since died."

For many years it has been known that the larger animals have a slow pulse rate, and vice versa. Thus the elephant, 25-28; horse and ox, 36-50; sheep, 60-80; dog, 100-120; rabbit, 150; mouse, 700

and canary bird, 1,000. However the heart and the heart-beat have no fixed relation to the size of the animal. The amount of driving work done is a principal factor. In a fish the heart need pump blood only to the gills; its weight is only $\frac{1}{10}$ of 1 per cent of the weight of the fish. In birds, on the other hand, there is a large amount of work to be done; their hearts are from 1 to 3 per cent of body-weight. The pigeon's heart weighs as much as that of a salmon fifteen times its size.

Warm-blooded animals must maintain a temperature higher than that of the surrounding air. They are constantly giving off heat to the surrounding environment and this makes more work for the heart. The smaller the animal, the larger is the *relative* area over which to give off heat. If the animal with the larger *relative* area cannot pump more oxygen-containing blood with each beat, its heart must pulsate more frequently. Thus the heart rate varies not only according to the size of the heart, but also in accordance with metabolism. The pulse rate seems to vary directly with the carbon dioxide output. Thus we have the ratios

$$\frac{\text{Mice}}{\text{Men}} = \frac{\text{CARBON-DIOXIDE OUTPUT } \frac{8.4}{0.6}}{\text{PULSE RATE } \frac{1008}{72}}$$

A series of observations for various birds and animals made by Florence Buchanan, (8) have verified this simple relationship.

The fact that the area of small objects is relatively greater in ratio to volume than the area of large objects of the same shape may be readily shown by noting area and volume for two cubes of different sizes. The area depends on the square of the diameter and the volume on the cube of the diameter; hence a reduction in diameter leads to an *increase* in the ratio of area to volume. By a similar con-

sideration of rectangular solids it may be illustrated that tall, slender people have greater surface area than short, rotund persons of the same weight. This gives a clue as to why the former tend to have a higher pulse rate than the latter. In the first example we have changed the size but not the shape; in the second example, the shape but not the weight.

The domestic animals such as the ox and the chicken usually have slow hearts and have been chosen by man so as to fatten easily. The race-horse and the

TABLE 1
Pulse rates and age (after Tigerstedt)

AGE	AVERAGE PULSE	MAXIMUM	MINIMUM
0	134	160	101
1	111	136	84
2	108	134	84
3	106	124	80
4	103	133	80
5-9	96	128	68
10-14	87	120	56
15-19	79	112	52
20-24	74	100	41
25-44	71	104	50
45-49	72	100	49
50-59	73	108	48
60-69	74	100	52
70-79	75	104	50
80 and over	77	98	63

deer represent the opposite tendency and have large hearts. The pulse rate among human beings doubtless varies according to the driving power exerted and the basal metabolism as well as the force of the central nervous system.

The pulse rate varies greatly in health according to age, sex, temperament, exercise or rest, emotional states, temperature, time of day, posture, atmospheric pressure and personal idiosyncrasy. During the pre-natal period the average number of pulsations per minute is about 150. The figures in Table 1 have been derived

from 2,500 examinations reported by Dr. Robert Tigerstedt (44), of the University of Helsingfors, Finland.

These figures have been represented graphically and the results are shown in Figure 1. The higher pulse rate in children is due in part to the smaller size of the body, i.e., large area in relation to volume, but is also related to the more active metabolism of the small and young individuals. It is evident that the pulse rate decreases as age advances until about age 25. In the above data there is a slight increase in the pulse rate after age 45, but other observers have noted either the opposite tendency or no change with advance in age. Quite clearly other factors than age are of distinct importance, since in a number of age-groups the maximum reading of pulse was at least twice the minimum.

In passing, it may be noted that the decreasing pulse rate during infancy and youth is accompanied by a corresponding increase in blood pressure. This inverse relationship does not usually continue into the later years of life.

The higher average pulse rate for women than for men is doubtless to be associated with their smaller average physique.

Dr. James Mackenzie (34) points out that the healthy heart is readily affected by the most trivial circumstances. Thus the exposure of the body to cold air slows the pulse by a few beats per minute. The addition of clothing by increasing warmth increases pulse rate. In slow walking a pulse of 68 may go up to 100, in quick walking to 140 and in running to 150 per minute. The pulse rate is usually more rapid in the evening than in the morning and is also higher after a meal, probably largely as a result of the addition of heat to the body through

food. Drinking hot water accelerates and drinking cold water retards the pulse.

In the year 1931 three large life insurance companies, the Metropolitan, New York Life and Equitable, contributed pulse rate data for 36,000 men and women who applied for life insurance. Of these 18 per cent were women. The averages

was 3.5 greater, and in the age-group 64-70, 2.5 less than for all ages. Similar age differences hold for females. At ages 15-63 the pulse rate for each sex was practically constant. The excess of the pulse rate for women over that of men ranged from .6 to 1.9 and averaged 1.1. It may be regarded as practically constant for all ages from 10 to 70.

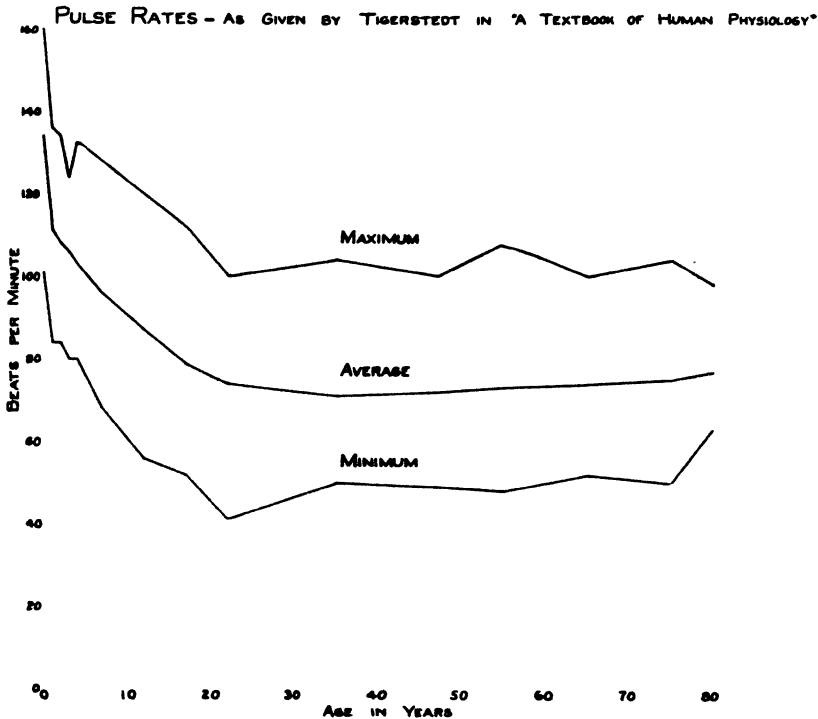


FIG. 1

were obtained in quinary age-groups from 10 to 70. These averages differ considerably from those which have been generally accepted by medical men throughout the world as representing pulse rates among the races of Northern Europe. The average found for white men was 74.7 and for white women 75.8 per minute. At age-group 10-14 the average for males

One of the companies gave pulse rates for substandard (i.e., under average) lives and also for Negroes. No significant difference could be discovered between the pulse rates of whites and Negroes nor between pulse rates of standard and substandard lives. This set of statistics is doubly interesting, because a few early observers such as Jousset

had recorded that African lives tended to have higher pulse rates than whites. That may have been due, however, to (a) the more primitive life of the natives, (b) a tropical environment, and to some nervousness upon having the pulse readings taken.

With respect to the pulse rates of different races, it is interesting to note that Dr. Hrdlička (26) found that the average pulse rates in healthy, adult North American Indians of certain tribes were decidedly lower than for white persons, being 5 to 20 beats slower, depending on the tribe. In the females the pulse was found to be generally quicker than in the males, the average difference amounting to about 6 beats.

The most remarkable result in the above figures, which form by far the largest volume of material which has been published on this subject, is the small difference between the pulse rates of men and women. For nearly a century the *Cyclopedia of Physiology* and other textbooks for medical men have relied largely upon the observations made by Dr. William Guy (19, 20, 21, 22) in 1838 and later. Upon the basis of these figures it has been accepted that the average pulse rate for an adult man is 72 and for a woman 80. It remains to be discovered whether the present averages are typical generally.

R. H. Britten and L. R. Thompson (6) obtained an average pulse rate of 81.1 for men in the garment, glass, pottery, foundry, steel, chemical, cigar, gas and cement industries. The authors stated, however, that this relatively high rate may have been largely due to the high proportion of foreignborn who from ignorance were nervous at time of examination. The rates of pulse for women were about two beats per minute higher than for men.

The question whether pulse rates vary

according to season, such as between winter and summer, has been touched upon in the literature, but without any substantial statistical basis. One life insurance company contributed in 1931 observations on the lives of 16,000 men and found average pulse rates of 74.8 in December, 74.6 in March, and 74.2 in July. These readings differ by only a fraction of a beat per minute, and the differences are obviously immaterial.

In this connection reference is made to an interesting paper by R. H. Britten and C. R. Wallace (7). The purpose of the study was to test the amount of variation found in any individual on different days. The normal course of pulse rate from day to day was found to contain an element of great variability. The probable error of an average pulse rate of 77.3 was found to be 6.2, so that it would be an even chance that any one reading would lie between 71.1 and 83.5. In fact the variability in pulse rate readings from day to day for a single individual was found to be of the same order of magnitude as a variation of the pulse rate in different individuals. Reading deviations such as 10 or 15 beats per minute from the true average might occasionally be expected for an individual without having any particular significance. The report was based upon 110 observations upon each of eleven men and eleven women.

There is very little published information as to the relation of pulse rate to height and weight. In 1926, R. H. Britten and L. R. Thompson (6) stated that for the same height the average pulse rate seemed to decrease slightly as weight increased. For an increase of 35 pounds there was a decrease of 2.5 beats.

Volkman (in Howell (25), p. 587) is quoted as saying "Pulse rates vary inversely as the five-ninth power of the

height." If this were true the following would be typical figures.

Height.....	4'0"	4'6"	5'0"	5'6"	6'0"	6'6"
Pulse rate...	90	84	79	75	71	68

This rapid *decrease* in pulse rate as height increases does not appear to have been substantiated statistically. Some tendency in that direction might be expected if persons of all ages were included, since children, before growth is attained, have higher pulse rates than during adult life. However, it may be noted that if height increased without change in weight, the pulse rate would be expected to *increase* since the surface area has increased

TABLE 2

Height, average weight and average pulse rates (ungraded and graded) of soldiers in the Philippines

HEIGHT (inches)	AVERAGE WEIGHT (lbs.)	NUMBER OF MEN	AVERAGE PULSE RATES	
			Ungraded	Graded
63 or less	132.9	27	79.0	79.3
64	134.7	114	80.3	79.8
65	139.9	157	80.0	80.4
66	141.9	187	81.5	80.9
67	144.4	225	80.4	81.2
68	147.2	251	82.3	81.6
69	152.7	127	82.6	81.7
70	155.6	80	80.2	81.7
71	159.0	40	81.5	81.9
72 and over	164.5	35	83.0	82.3

without a greater volume, as was noted earlier in this paper.

In the usual circumstances the weight of the individual increases with his height, and average pulse rates have been obtained for a group of healthy soldiers in the Philippines arranged in this manner (see Chamberlain (10)). The average age of the 1,243 men was 27. The final column in the foregoing table has been added by grading the pulse rates in accordance with Henderson (see Bowerman (5)). It shows upon the average an *increase* in pulse rate of one beat per minute for each three inches of increase in height.

The above figures appear to be the only ones which have been published on this subject. It should be observed that they do not accord with the hypothesis that the average pulse rate is generally lower among those of larger physique. The observations were made in the tropics and the average pulse rate, 81, was six beats greater than that of the much larger group of insured men reported above.

The effect of exercise upon pulse rates has been investigated in considerable detail in Germany, particularly by Christ (11) and F. Tewildt (43). More clear-cut conclusions were given, however, by George Kolb (32). He made observations upon the pulse rates and blood pressures of oarsmen during and at the end of a training period of four weeks. His chief conclusions were as follows:

(A) Under normal conditions of training the pulse rate fell during the four weeks from 70 to 80 per minute to about 60 to 45 beats per minute. The blood pressure increased to 160 to 185 mm.

(B) In cases of overtraining and lost condition the pulse rate increased again to 90 to 100 beats per minute while the blood pressure fell to 120 mm.

Signs of a healthy development in athletic training are therefore a slow action of the heart, a high blood pressure and a strong pulse. Signs of an unhealthy condition are an accelerated action of the heart, a low blood pressure and a weak pulse.

Associated with the results of exercise are the milder effects of a change in posture. A number of investigators from the days of William Guy to the present have noted the changes in pulse rate which follow a change as from recumbency to a standing posture. One of the most carefully executed papers was based upon pulse rate readings of aviators in the Medical Research Laboratory and

School for Flight Surgeons at Mitchell Field, Long Island (Schneider and Truesdell (39)). The following table summarizes their data regarding postural change among 2,000 men of average age 25.

TABLE 3
Postural pulse rate change shown by the median

PULSE RATE IN RECUMBENCY	INCREASE ON STANDING		PULSE RATE STANDING	DECREASE ON RECLINING	
	104 men physically fit	1000 men unselected		104 men physically fit	1000 men unselected
60	18	21	60	—	3
63	15	21	63	3	3
66	15	18	66	3	6
69	15	18	69	3	6
72	12	18	72	6	9
75	12	18	75	9	9
78	12	18	78	9	12
81	9	15	81	12	12
84	6	15	84	15	15
87	6	15	87	15	15
90	—	15	90	15	18
93	—	12	93	15	18
—	—	—	96	15	21
—	—	—	99	18	21
—	—	—	102	—	21
—	—	—	105	—	24

Since the pulse rate varies according to the vigor of the body and the rate of metabolism, it may be expected to vary also with respect to occupation. To throw some light upon this question, a large life insurance company has contributed pulse rates of 7,060 men arranged in broad occupational classes as shown in table 4.

The average pulse rate of the entire group was 74.7.

The men in the above table were all granted life insurance at standard rates and at ages 20 to 65 only. The tendency to a lower pulse rate among those engaged in outdoor activity may be noted, and more particularly among those in the heavier types of muscular work.

TABLE 4
Pulse data by occupational classes

OCCUPATION	NUMBER OF CASES	EXCESS OF PULSE RATE OVER AVERAGE OF ALL CASES
Agriculture.....	604	-1.0
Extraction of minerals.....	80	-1.1
Manufacturing.....	981	+1.2
Construction.....	535	+1.2
Skilled occupations, n.e.c.	230	-1.2
Transportation.....	763	-1.5
Trade.....	2,064	+1.4
Public service.....	72	-1.3
Professional service.....	772	0
Domestic and personal service..	354	+1.5
Clerical occupations.....	475	+1.0
Non-gainful occupations.....	130	-1.6
	7,060	0
Light work.....	4,620	+1.3
Heavy work.....	2,440	-1.6

The possible significance of pulse rates in relation to disease has been touched upon by several investigators. Probably the layman would associate a rapid pulse with a nervous temperament and tubercular tendencies; while a slow pulse would accord with a phlegmatic tone. Dr. Eugene F. Russell (38), in 1924, stated that a pulse persistently above 90 would usually indicate some organic trouble such as tuberculosis, toxic goitre, nephritis, or possibly the excessive use of alcohol, tobacco or other stimulants. Paroxysmal tachycardia is also occasionally found under these conditions. "A slow pulse such as 30 to 50 may indicate heart block, myocarditis, aortic stenosis, some change in the blood vessel wall or cerebral tumor."

On the other hand, J. J. Walsh (45) stated in 1900 that "the most frequent cause of slow pulse is gastro-intestinal disturbance including cancer of the digestive tract." He cited the case of a woman aged 31 with a pulse rate of 36, who was

nervous and high strung and not at all phlegmatic.

Dr. Florence Buchanan (8) thought that rapid pulse is more indicative of nervous and respiratory troubles than of circulatory impairments. This, I believe, is the prevailing opinion.

In the life insurance practice of the United States and Canada, a pulse rate between 55 and 90 per minute is generally looked upon as being acceptable at standard rates of premium.

In the *Medical Impairment Study* (1) it was found that the mortality on cases with a persistent pulse of between 90 and 100 beats per minute was about 150 per cent of the standard. A small group of cases accepted with a persistent pulse of over 100 beats per minute indicated about the same percentage of standard mortality, but the selection was probably severe on these latter cases.

The mortality under policies with a persistent pulse rate between 55 and 65 beats per minute was about 80 per cent of the standard. Apparently a moderately slow pulse is a good factor as far as mortality is concerned. Cases with persistent intermittent pulses and those with irregular pulses showed a higher than average mortality.

SUMMARY

When the *Medical Impairment Study* (1929) was in course of preparation during 1931, the investigation of abnormal pulse directed attention to the general subject of pulse rates. Some of the data dealing with pulse rates which were brought

together in connection with this medical research are here reviewed.

The classic paper on the subject is that of Dr. William A. Guy (19) of London published in 1838. He studied the pulse rates of 100 healthy men, and observed that the rates varied when the subject was in a standing, sitting or horizontal position. He found that the pulse rate went up after taking a meal, and also that the pulse rate in the evening differed from the rate in the morning. For many years the textbooks and encyclopedias have as a result given 72 as the average pulse rate for men, and 80 for women. This results in an excess of 8 per minute for women as contrasted with only 1 per minute in the study of 30,000 lives made in connection with the *Medical Impairment Study*. The average pulse rates found among the 30,000 lives were 74.7 for men and 75.8 for women.

For years it has been known that the larger animals have a slow pulse rate and vice versa. Thus the elephant, 25-28; horse and ox, 36-50; sheep, 60-80; dog, 100-120; rabbit, 150; mouse, 700; and canary bird, 1,000.

It has been brought out by various writers that the human pulse rate varies greatly in health according to age, sex, temperament, exercise or rest, emotional states, temperature, time of day, posture, atmospheric pressure and personal idiosyncrasy.

Studies have been given showing the pulse rates of men in various occupations, and also of individuals at varying builds.

LIST OF LITERATURE

1. ACTUARIAL SOCIETY OF AMERICA AND ASSOCIATION OF LIFE INSURANCE MEDICAL DIRECTORS. *Medical Impairment Study* (1929). New York (Actuarial Society of America), 1931. Pp. vi + 172.
2. BARCOCK, ROBERT H. The pulse as a guide to the life insurance examiner. New York (Lea Brothers and Co.), 1904. Pp. 11. Reprinted from *Medical News*, New York, April 23, 1904.
3. BORDEU, THEOPHILE DE. Recherches sur le

- Pouls, par rapport aux crises. 2nd edition. Paris (Didot Jr.), 1772. 2 volumes. Pp. 356 + 388.
4. BOUILLAUD, J. B. Nouvelles Recherches sur l'Analyse et la Théorie du Pouls. Paris, 1873.
 5. BOWERMAN, WALTER G. Henderson's mechanico-graphic method of graduation. *Trans. Actuarial Society of America*, Vol. 38, pp. 7-11, 1937.
 6. BRITTEN, R. H., AND THOMPSON, L. R. A health study of ten thousand male industrial workers. Statistical analysis of surveys in ten industries. *Public Health Bulletin*, No. 162, pp. 44-52, 1926.
 7. —, AND WALLACE, C. R. Consecutive readings of pulse rate under a small group of clerks. *Public Health Reports*, Vol. 45, pp. 3128-3135, 1930.
 8. BUCHANAN, FLORENCE. Significance of pulse rate in vertebrate animals. *Annual Report of Smithsonian Institution*, 1910, pp. 487-505.
 9. BURLAGE, S. R. Blood pressure and heart rate, in girls, during adolescence. A preliminary study of 1,700 cases. *Proceedings of the Society for Experimental Biology and Medicine*, Vol. 19, pp. 247-248, 1922.
 10. CHAMBERLAIN, W. P. A study of the systolic blood pressure and the pulse rate of healthy adult males in the Philippines. *Philippine Journal of Science*, Vol. 6, No. 6, Section B, Medical Sciences, pp. 467-482, 1911.
 11. CHRIST, H. Über den Einfluss der Muskelarbeit auf die Herztaetigkeit (The Influence of Muscular Exertion on the Action of the Heart) *Leipzig* (J. B. Hirschfeld), 1894. P. 43.
 12. CRIPPS. Pulse Rates for English woman. 1924.
 13. DELAUNAY. Etudes de Biologie Comparée. 2nd Partie—Physiologie. P. 47, 1878.
 14. ELLIS, HAVELOCK. Man and Woman. 6th edition. London (A. and C. Black), 1926. Pp. xxiii + 563. [Pp. 271-273.]
 15. ENCYCLOPEDIA, NEW INTERNATIONAL. Pulse.
 16. FLACK, MARTIN, AND HILL, LEONARD. A Textbook of Physiology. London (E. Arnold), 1919. Pp. viii + 800. [P. 216.]
 17. GILBERT, J. A. *University of Iowa studies in psychology*. Vol. 1, p. 32, 1897.
 18. GRAVES, ROBERT J. On the effects produced by posture on the frequency and character of the pulse. *Dublin Hospital Reports*, Vol. 5, pp. 561-571, 1830.
 19. GUY, WILLIAM A. The effect produced upon the pulse by change of posture. *Guy's Hospital Reports*, Vol. 3, pp. 92-110, and 308-320, 1838.
 20. —. On the diurnal variations of the pulse. *Guy's Hospital Reports*, Vol. 4, pp. 63-74, 1839.
 21. —. Observations on the pulse in phthisis pulmonalis. *Guy's Hospital Reports*, Vol. 4, pp. 369-380, 1839.
 22. —. The Pulse. In: *Cyclopaedia of Anatomy and Physiology*. Edited by R. B. Todd. London (Longman, Brown, Green, Longmans and Roberts). Vol. IV, pp. 181-194, 1847-1849.
 23. HALLOCK, MARY. Pulse and rhythm. *Popular Science Monthly*, 1903.
 24. HARDEN, JOHN M. B. Observations on the pulse and respiration. *American Journal of Medical Science*, Vol. 5, pp. 340-344, 1843.
 25. HOWELL, WILLIAM H. A Text-book of Physiology. 8th edition. Philadelphia and London (W. B. Saunders Co.), 1921. Pp. 1051.
 26. HRDLÍČKA, ALB. Physiological and medical observations among the Indians of south-western United States and northern Mexico. Washington (Gov. pr. off.) 1908. Pp. ix + 460. In: *Smithsonian Inst. Bur. Am. Eth. Bull.* 34.
 27. —. The Old Americans. *Baltimore* (Williams & Wilkins Co.), 1925. Pp. xiii + 438. [Chapter V.]
 28. KELLOGG, T. H. The Pulse in Insanity. *Geneva*, N. Y. (W. F. Humphrey), 1895. Pp. 13.
 29. KIMBER, D. C., GRAY, C. E., AND STACKPOLE, C. E. Textbook of Anatomy and Physiology. Tenth edition. New York (Macmillan Co.), 1938. Pp. x + 643. [Pp. 314-316.]
 30. KNOX, ROBERT. On the relation subsisting between the time of the day, and various functions of the human body; and on the manner in which the pulsations of the heart and arteries are affected by muscular exertion. *Edinburgh Medical and Surgical Journal*, Vol. 11, Pp. 52-65 and 164-167, 1815.
 31. —. Physiological observations on the Pulsations of the heart, and on its diurnal revolution and excitability. *Edinburgh Medical and Surgical Journal*, Vol. 47, pp. 358-377, 1837.
 32. KOLB, GEORGE. Contributions towards the Physiology of a Maximum of Muscular Exertion.
 33. LAMSON, P. D. The Heart Rhythms. *Baltimore* (Williams & Wilkins Co.), 1921. Pp. 100.
 34. MACKENZIE, JAMES. The Study of the Pulse. New York (Macmillan Co.), 1902. Pp. xx + 325.
 35. NIBELL, JAMES. New and Extraordinary Observations concerning the Prediction of Various Crises by the Pulse. London (Society of

- booksellers for promoting learning), 1741. Pp. xxviii + 153.
36. PYLE, W. L. A Manual of Personal Hygiene (Seventh Edition). *Philadelphia* (W. B. Saunders Co.), 1917. Pp. xiv + 555. [Pages 495-6 in the Appendix.]
 37. ROSELI. *Arch. per l'Antrop.* P. 46 ff., 1880.
 38. RUSSELL, E. F. Life Insurance Examination edited by F. W. Foxworthy. *London* (Henry Kimpton), 1924. Pp. 738. [Chapt. 17—Examination of the Heart and Blood Vessels, Pp. 169-196.]
 39. SCHNEIDER, E. C., AND TRUMBELL, DOROTHY. A statistical study of the pulse rate and the arterial blood pressure in recumbency, standing and after a standard exercise (Mitchell Field, L. I., Medical Research Laboratory and School for Flight Surgeons). *American Journal of Physiology*, Vol. 61, p. 429, 1922.
 40. STARLING, E. H. Principles of Human Physiology. (2nd edition) *Philadelphia* (Lea and Febiger), 1915, xiv + 1271. [Page 981.]
 41. STOCKS, PERCY, AND KARN, M. N. Blood pressure in early life. A statistical study. *University of London. University College. Drapers' Company Research Memoirs. Studies in National deterioration.* Vol. 11, pp. 1-88, 1924.
 42. TAYLOR, SKYMOUR. Remarks on the slow heart. *The Lancet*, Vol. I for 1891, pp. 1247-1249, 1891.
 43. TEWILDT, F. Influence of body motion on the pulse of normal people (in German). *Archiv. f. Physiologie*, 1903. [Bibliography useful.]
 44. TIGERSTEDT, ROBERT, A. A. A Textbook of Human Physiology. Translated from 3rd German edition and edited by John R. Murlin. *New York and London* (D. Appleton and Co.), 1906. xxxi + 751.
 45. WALSH, J. J. Persistent slow pulse. *Medical News*, Vol. 77, pp. 736-737, 1900.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Mrs. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

ADAPTIVE COLORATION IN ANIMALS.

By Hugh B. Cott. With an Introduction by Julian S. Huxley. Oxford University Press, New York. \$8.50. 9 $\frac{1}{2}$ x 6 $\frac{1}{2}$; xxxii + 508; 1940.

The force of the facts and arguments used in this work is cumulative in effect. Taken singly as isolated phenomena, they may appear to be insignificant. Taken together, and considered in relation to one another, and to kindred phenomena in other fields, they present a body of evidence which makes it appear that adaptive coloration is one of the chief attributes of the higher animals, and has been, indeed, one of the main achievements of organic evolution.

In addition to the immense body of examples presented, Cott has given the latest experimental evidence that there is a selective advantage accruing to those organisms with concealing, warning, or imitative coloration. Persons who continue to oppose the selective theory will find themselves squirming, to say the least, under the force of his arguments. The book is a scholarly treatment of protective coloration in every one of its aspects and in detail, showing how the coloration is correlated with behavior, life histories, and variable environment of the organism under consideration. The volume is greatly enhanced by numerous excellent photographs taken under natural conditions. There is a bibliography of 685 titles and a 24-page index.

EMBRYOS AND ANCESTORS.

By G. R. de Beer. The Clarendon Press, Oxford; Oxford University Press, New York. \$2.50. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; x + 108 + 3 plates; 1940.

This volume is a revision of *Embryology and Evolution* (cf. Q.R.B., Vol. 5, p. 465). The author states in the preface that "he has seen no reason to alter the plan of my former book in the slightest degree." The revision consists of the enlargement of the various divisions of the book by the addition of new facts pertaining to the relationship existing between embryology and evolution which have been brought to light since the previous volume was issued in 1930. An important work for students of advanced biology.



STRUCTURAL ADAPTATIONS IN THRASHERS (MIMIDAE: GENUS TOXOSTOMA) with Comments on Interspecific Relationships. University of California Publications in Zoology, Vol. 42, No. 7.

By William L. Engels. University of California Press, Berkeley. 75 cents. 10 $\frac{1}{2}$ x 6 $\frac{1}{2}$; 60; 1940 (paper).

Two marked tendencies of behavior in this form are ground foraging and running rather than flying as a means of locomotion. Structural characters associated with the digging habit are of three sorts:

preadaptations, incidental adaptations, and primary adaptations. In association with the tendency to run there are well-marked modifications in the structure of the wing, chiefly in the proportions of the wing segments.



GENETICS

EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES. I. *Effect of Varied Environments on Western North American Plants.* Publication No. 520.

By Jens Clausen, David D. Keck and William M. Hiesey. Carnegie Institution of Washington, Washington, D. C. \$3.50. 10 x 6½; vii + 452; 1940 (paper).

The difficulty of defining exactly what constitutes a species is recognized by all systematic biologists, and it is now pretty generally conceded that the only way to reach a solution of this problem is by experiment. The authors of the present work have undertaken some large scale experimentation on native California plants, the first phase of which work they now give in this report.

It is well known to everyone who has ever taken the trouble to observe it that when a plant (or an animal as well, for that matter) is widely distributed, it tends to break up into differentiated local forms. These local forms are of two distinct types, according as to whether the features that characterize them may be transmitted by heredity or not. A change in the environment may produce a change in the organism; such change is ordinarily not heritable, and is designated in the present work as a modification. But some species are divided into genetic strains (which the authors call ecotypes) which react differently to the environment. These are distinguished by heritable features, and the effect of the environment may be to preserve some at the expense of others. It must also be recalled that the features that characterize ecotypes may be somatic or cytological; they may even be physiological.

The technique employed by these investigators was first to select eleven different stations, one on the Pacific coast, one

at Mono Lake, and others at various intermediate points, running up to an altitude of 3500 feet in the Sierras. At these stations were planted various wild plants, belonging chiefly to the genera *Potentilla*, *Horkelia*, *Zauschneria*, *Penstemon*, *Achillea*, and *Artemisia*. A few other genera were also represented. When plants native to one station were transplanted to other stations, they developed changes in the form of the leaves, length of stem, etc., flowered at a different date, and exhibited various degrees of polyploidy.

A tremendous amount of experimentation is covered in this report. There are also several appendices, one of which is a list of chromosome numbers that have been determined in upwards of 100 different subspecies; another is a list of 35 new names. Finally, there is a bibliography of six pages and an index of nine. The work is well supplied with photographs, diagrams, and tabulations.



PREFACE TO EUGENICS.

By Frederick Osborn. Harper and Bros., New York and London. \$2.75. 8½ x 5½; xi + 312; 1940.

With increasing education of the masses and the recent rapid advance of specific knowledge through research in the biological and social sciences has come the realization that eugenic ideals are not mere distant visions but are present possibilities. It is true, as Osborn points out, that the eugenic policy must be a conservative policy, conditioned by the slow process of social education, but "the broader aspects of eugenic proposals can now be outlined in terms acceptable both to the scientist and to the layman who is interested in other aspects of human progress. The more detailed applications of eugenics can be refined and made effective as a result of experience and with the further advance of science."

This book discusses the existing knowledge upon which our eugenic policies must be based. The author devotes considerable space to the value of population studies, an aspect of the problem the high significance of which is seldom

taken into account. The outstanding place of heredity in eugenics is adequately presented, but not to the exclusion of the environmental factors with which genetics is inextricably interwoven. Numerous positive suggestions for human betterment are given, along with the means of carrying out these suggestions through the parents, schools, doctors, clergymen, welfare workers, and those engaged in scientific research. The soundness and scientific bases of the author's arguments, coupled with his clarity of writing should make this volume equally acceptable to the biologist, the sociologist, and the lay reader.



ORGANISERS AND GENES.

By C. H. Waddington. *The University Press, Cambridge and Macmillan Company, New York.* \$3.00. $8\frac{1}{2} \times 5\frac{1}{8}$; x + [2] + 160; 1940.

One of the most perplexing biological problems of recent years is the nature of the causal mechanism of development. Exploration of the problem has been progressing in two fields—embryology, which studies the activity of organisers in the process of differentiation; and heredity, which deals with the genetic factors antecedent to development of adult structure. There has already been some attempt at synthesis of these fields toward a solution of this complex problem, and Waddington's book further bridges the gap. The early pages discuss experiments on organisers and their action among various vertebrates, the activation and chemical nature of the evocator, and the competence of tissues. The author next turns to the effects of genes or of substances produced by genes. After a discussion of growth and developmental patterns there is a final chapter on the theory of organization. Although the known facts about differentiation are meager, Waddington has a clear understanding of the problems involved which he transmits to his readers by frequent use of analogy to similar situations in other scientific fields. The volume contains concise definitions of all terms and an extensive bibliography.

THE BREEDING OF HERBAGE PLANTS IN SCANDINAVIA AND FINLAND. *Imperial Agricultural Bureau Joint Publication No. 3. Imperial Bureau of Plant Breeding and Genetics, School of Agriculture, Cambridge.* 4s. $9\frac{1}{2} \times 7\frac{1}{2}$; 123 + 2 folding tables; 1940 (paper).

Since the early years of the present century the Scandinavian countries have been doing important work in the breeding of herbage plants. In this report, which is in the form of a symposium, well-known Swedish and Finnish specialists discuss the following: (Sweden) (1) Herbage plant breeding in Sweden; (2) The application of cytology to herbage plant breeding; (3) Luzerne breeding in Sweden; (Denmark) (1) Improvement of herbage plants in Denmark; (2) Some breeding experiments with timothy; (Norway) (1) Selection and inbreeding in red clover and timothy; (Finland) (1) Red clover breeding in Finland. A summary, preceding the separate articles, indicates the lessons to be drawn from the experimental work. The different crops are treated separately, most space being given to red clover and timothy. Much tabular matter and reference lists are included in the separate articles. The report concludes with lists of the stations where the plant breeding and research work is being done, their locations being indicated on two maps of the Scandinavian region.



A STUDY OF METHODS IN BARLEY BREEDING. U. S. Department of Agriculture. *Technical Bulletin No. 720.*

By H. V. Harlan, M. L. Martini and Harland Stevens. *Government Printing Office, Washington.* 5 cents. $9\frac{1}{8} \times 6$; 25; 1940 (paper).

For the purpose of developing, if possible, a strain of barley superior in growth, yield, and resistance to disease, 28 parent varieties were collected from various parts of Europe, Asia, Africa, and the United States, and an enormous program of breeding and selecting was pursued over a period of 7 generations. The analysis of yields of the progeny of 379 crosses as well as that from the progeny of a composite lot resulting from the mix-

ture of the same 379 crosses form the basis for this monograph. The authors admit that the present investigation did little more than clarify the experimental procedure in their own minds, and that actually more questions were raised than were answered. They hope, however, that by further experimentation with multiple hybrid crosses they may arrive at their desired superior strain of barley.



GENERAL BIOLOGY

FUNDAMENTALS OF BIOLOGY: *Animal and Plant. Second Edition.*

By William C. Beaver. C. V. Mosby Company, St. Louis. \$4.00. 8½ x 5½; 889; 1940.

Beaver has written this text with the hope that it will be of greater service to the instructor and the student by presenting the more important biological facts briefly enough to permit a complete comprehension of the subject as a whole and also to serve as a skeleton to which additional data may be added. The essentials of biology are so arranged as to permit an easier and more effective mastery of the fundamentals. In brief, the book is designed to "help the instructor help the student to help himself." This text offers the teacher many worth-while advantages. It is large enough that it can serve as a classroom text and at the same time contains much reference reading for the course in general biology. There is also the proper balance between animal and plant biology. Emphasis has been placed on the application of biology in the fields of health, wealth, and conservation. The illustrations have been carefully selected and annotated. The appendix provides definitions of biological theories and principles, important prefixes and suffixes used in biology, an extensive glossary, and a list of references for both zoology and botany. The complete index has been prepared with especial care.



INTERMEDIATE BIOLOGY.

By W. F. Wheeler. With a Foreword

by Eric Lucas. Chemical Publishing Co., New York. \$6.00. 8½ x 5½; xiii + 530; 1940.

It is the purpose of this book to overcome the treatment of zoology and botany as separate fields and to show the similarities between the two in every branch of biology. The first two sections describe the anatomy of representative forms of animal and plant life. Following this, the two kingdoms are compared as to cellular structure, physiology, embryology, evolution, and ecology. The aim of the book is admirable, but one cannot escape the conclusion that such a comparison in a text book works at odds against the best interests of the student. True, it tends to unify biology as a whole, but only at the sacrifice of unity within each branch of the science. It is beyond the scope of such a text to present all that should be said about both the plant and animal kingdoms even in a fundamental course. As a result, much essential material is omitted. As an example, less than nine pages are devoted to the mechanism of inheritance. The volume is adequately illustrated and contains thorough index.



THIS LIVING WORLD: A College Course in Science.

By C. C. Clark and R. H. Hall. Drawings by Louise W. Germann. McGraw-Hill Book Co., New York and London. \$3.25. 9 x 6; x + 519; 1940.

This text is the first of two volumes that constitute the bookish side of a course in general science offered, at New York University, to students whose aims are cultural and exploratory. A companion volume, *This Physical World*, will be published soon. The first volume centers its emphasis on the human body and its functioning, but the scope of the book is sufficiently extended to link animate nature to every phase of the domain in which it lives. The book opens, for instance, with a brief account of Maffei's *Scala Naturale*. It is important to bear in mind that this book is addressed to the dilettante reader. Its contents, accord-

ingly, are romanticized. There is, for example, the Norse story of Iduna, the goddess of youth. It is remarkable what a long way a very little biology can go, when emphasis is placed on making it attractive even to those who are not likely to be interested.



UNRESTING CELLS.

By R. W. Gerard. Harper and Bros., New York and London. \$3.75. 8½ x 5½; xv + 439; 1940.

The intent throughout this fascinating volume has been to present the problems that biologists have recognized, the evidence they have accumulated and organized in attempting to solve these problems, the answers which they can give today, and particularly the careful manner in which they reach and check their conclusions. The book is not intended as a complete essay on biology, but is a most appealing and acceptable popularization of certain phases of the subject. The emphasis is not so much upon the facts themselves, but rather upon the various techniques employed by scientists in ascertaining these facts. Some of the rather unique chapter headings are: Odyssey of an amoeba, Architecture in miniature, Master craftsmen, Molecular traffic, Fuel for the lamp of life, Oaks from acorns, and Inherited molecules. The illustrations are a striking feature of the book. There is no bibliography, but a good index has been prepared.



HUMAN BIOLOGY

THE LIFE, LETTERS AND LABOURS OF FRANCIS GALTON. Vol. I, *Birth 1822 to Marriage 1853*; Vol. II, *Researches of Middle Life*; Vol. IIIA, *Correlation, Personal Identification and Eugenics*; Vol. IIIB, *Characterisation, Especially by Letters, Index*.

By Karl Pearson. The Macmillan Co., New York; University Press, Cambridge. \$28.00 for the set. 11 x 7½; Vol. I, xxiii + 246 + 66 plates; Vol. II, xi + 426 + 54 plates; Vol. IIIA and Vol. IIIB, xii + 673 + 59 plates; Vol. I,

1914; Vol. II, 1924, Vol. IIIA and Vol. IIIB, 1930.

The first of these three volumes (in two parts) appeared in 1914; the second, in 1924; and the third, in 1930. In view of the fact that the complete set is now available at a price considerably below the original, we bring this important work—a monument not only to the subject but also to the author—to the reader's attention.

In the introduction to the final volume Pearson explains that he is not a man of letters (a statement which will not meet with universal agreement) and that in writing this book he was actuated solely by the desire to tell the story of his teacher and friend. One reason for taking this position was that he was too close to Galton to do for him what, for instance, West did for Darwin, or Stejneger for Steller. The size of the work bears witness to Pearson's desire to make it as exhaustive as possible. It is a source book for the scholar rather than a narrative for the general reader. The Galton family preserved a wealth of material in the shape of correspondence, both by and to Sir Francis, and this they generously submitted to Pearson with permission to publish, a permission of which he availed himself extensively, for he realized the importance of preserving these documents for posterity.

The greater part of the first volume is occupied by a discussion of Galton's ancestry—a thoroughly consistent way to begin the life story of the founder of the science of eugenics. Everyone knows that Francis Galton was the grandson of Erasmus Darwin and the cousin of Charles Darwin, but it is not so well known that he was also the descendant of Robert Barclay, the apologist, or that he was related to Elizabeth Fry, who frequently visited the Galton family, and exercised a great influence on Francis in his early youth.

Francis Galton, ninth child of Samuel Tertius Galton and Violetta (Darwin) Galton, was born February 16th, 1822, at The Larches, near Sparbrook, Birmingham, in a house built by Withering, the botanist, and occupied subsequently by Priestley, the chemist. His early educa-

tion was in charge of his eleven-year-old sister, Adèle, also a gifted child. At the age of two he could read, sign his name at three, recite most of Scott's "Marmion" at five, and read the *Iliad* in the original at six.

Lack of space precludes discussion of Galton's formal education at Boulogne, Birmingham, and Cambridge, where he studied medicine to please his father, mathematics to please himself, and classic languages to please his teachers; or of his trip to Giessen, ostensibly to study organic chemistry under Liebig, but which he converted into a pleasure jaunt to the Bosphorus and the Mediterranean; or of his later expedition to Africa to settle the differences that had arisen between the natives and the Boer migrants who had settled in British territory. Although all these phases of Galton's activity are adequately considered by Pearson mere mention of them must suffice here, for his scientific career did not really begin until after his marriage to Louisa Butler on August 1st, 1853, when he settled down to devote himself to the scientific pursuits that were destined to occupy his attention during the remainder of his long life.

In the next few years he investigated such diverse matters as solar eclipses, heliography, relief maps to be made in pairs and viewed through a stereopticon, meteorological maps, anticyclones (which he discovered and named), the possibility of constructing a pantagraph that would reduce different scales simultaneously in different ratios, the practical utilization of wave power, mensuration of the altitude of clouds, and even spiritualism. His old interest, mathematics, was not neglected, but it was now made to serve the biological sciences, chiefly anthropology. The outcome of the mathematical study of human inheritance was the epoch-making *Hereditary Genius* which won the praise of Darwin and made inevitable the science of eugenics.

The rest of Galton's activities, such as his study of finger prints, composite photography of criminals to see if a "criminal type" could be isolated, the establishment of the Eugenics Laboratory at the University of London, as well as the more personal side of his biography,

the passing of his contemporary friends and the relatives of his own generation, have received the treatment they merit. In his later years he received the medal of the Linnean Society and was knighted by King Edward VII.

Galton's method, according to Pearson, was to formulate his problem, and then to devise his experiments to throw light on it. In this respect he was the antithesis of Darwin, who first accumulated his observations and then let his imagination play on them. The difference between Newton and Bacon is roughly parallel—it is perhaps that between the mathematical and biological temperaments.

Pearson did an admirable work in preserving for future generations a living portrait of one of the most significant and versatile figures of the nineteenth century—the associate of Darwin, Spencer, Huxley, Wallace, Tyndall, and Carpenter, all of whom he outlived. The book has an excellent index of forty pages, and its wealth of plates adds greatly to its value.



WHY FRANCE LOST THE WAR: A Biological and Economic Survey.

By A. Reishinger. Veritas Press, New York. \$1.25. 7½ x 5½; 75; 1940.

The unexpected collapse of the French nation in a war largely of its own choosing has engendered a lot of more or less nonsensical speculation as to just what happened. The present work forms a pleasing contrast to most of these, for it contains nothing of a speculative nature. In it the author merely discusses the demography of France, and shows that the present condition is the inevitable result of the first world war.

Under Louis XIV one out of every three Europeans was a citizen of France. At the turn of the century this proportion was somewhat reduced, but France was still the most populous European state. Today only one European out of twelve is a French citizen, and Russia, Germany, Great Britain, and Italy can boast larger populations.

But this is not the only difference in demography between France and Ger-

many. There is also a difference in distribution among age groups. The non-productive groups, both children and aged, constitute a larger proportion of the total population in France than in Germany. And finally there is a difference in the replacement rate. While in both countries the population is increasing, the increase in France is dependent upon immigration. Except for immigration the French population could not maintain itself.

All this has a direct bearing upon the size of the army that either nation could maintain in the field. If both nations maintained equal armies, the French army would represent about three times the proportion of the productive population as would the German army. And if both armies suffered equally the German population could supply replacements much more rapidly than could the French. This would hold good not only for the armies actually in the field, but for that part of the population that remains at home engaging in gainful occupations to supply wealth, foodstuffs, and other needed commodities to support the army.

The author is a German and his viewpoint is that of the modern rulers of Germany. He puts the entire responsibility for the present war on Great Britain, saying that Russia, Germany, Italy, and France could have adjusted their vital interests sensibly and without difficulty had not Great Britain undertaken a coalition war against Europe, the tragedy of which was the alignment of France with the wrong side. This thought, reiterated more than once in the book, is likely to influence the thoughtful reader to question the author's intellectual competence to pass judgment on the collapse of France, but if the thoughtful reader can forget the prejudices, and overlook the ill-disguised attempts at propaganda of the author, he will be likely to conclude that so far as the purely factual conclusions are concerned, the author has convincingly proved his thesis.



HUGH YOUNG, *A Surgeon's Autobiography.*
By Hugh H. Young. Drawings by William

P. Didusch. Harcourt, Brace and Co., New York. \$5.00. 9½ x 6; xii + 554 + 6 plates; 1940.

Students of American history will be interested in the first 88 pages of this book. Hugh Young's grandfather fought for the republic of Texas, was a colonel in the Mexican War and a general in the Civil War, and his son, father of the surgeon, commissioned brigadier general at the age of twenty-six, was severely wounded and captured in the defense of Atlanta. After the war the two generals returned to San Antonio, Texas. San Antonio was at that time one of the liveliest and woolliest of the Western towns and here the autobiographer was born and spent his boyhood. By the time he entered the University of Virginia, where he earned his B.A., M.A., and M.D. within the space of four years, he had already had experience as a newsboy, horse trainer, athlete, carpenter and mechanic (his proficiency in these latter trades stood him in good stead later in devising new instruments, and provided him also with his first lesson in the deceits of business—he never did collect the \$6.50 a friend promised him for a buggy body he made at the age of fifteen), printer, editor, and cartographer. With the \$40 fee for his first operation in San Antonio he bought a ticket for Baltimore, where he continued his studies in surgery, served for a few months as bacteriologist at a children's sanitarium, assisted Dr. Halsted on the surgical staff of the Johns Hopkins Hospital and (two years later) was put in charge of the department of genito-urinary surgery, the specialty to which he has devoted a long and distinguished service and in which he won international fame.

About a quarter of the book is devoted to technical details of urological cases and various operations which illustrate his new techniques and instruments. This part, which is likely to be skipped by the squeamish, is illustrated with 103 excellent anatomical and surgical drawings by William Didusch.

Of more general interest are the descriptions of his patients (Diamond Jim Brady, who out of gratitude made possible the Brady Urological Institute, heads the

list), and friends, his service overseas with the A.E.F., his work on the venereal disease problem in the British, French and United States armies, his extensive travels, and his active contributions to the cultural life of Baltimore.

Although this most interesting and frank autobiography interspersed with amusing anecdotes will be of primary interest to medical men, it is bound to find a wider circle of readers.



EDUCATION AND THE BIRTH-RATE. *A Social Dilemma.*

By Grace G. Leybourne and Kenneth White.
With a Foreword by A. M. Carr-Saunders
and an Introduction by R. H. Tawney.
Jonathan Cape, London. 8s. 6d. net.
8 x 5½; vii + 375 + 9 folding tables;
1940.

During the last fifty years in most countries there has been a remarkable increase in the number of persons who receive a secondary school education or professional training. This phenomenon, as all realize, tends to raise the cultural level of the population. However, and in addition, other problems are created and these are especially evident in times of economic or political upheaval. The authors for the first time examine these problems with respect to England. In their opinion the desire for a higher education results mainly from the combined manifestations of snobbery and of the hope for an improved socio-economic status. The first general consequence is that parents attempt to limit the number of offspring. The second and most important consequence is that technically untrained but cultured (?) youths are dumped on a labor market which has no demand for such a commodity. Other consequences are (a) the need for more schools, and (b), specifically for England, the threat to the existence of private schools from the increased competition of government institutions. These inferences have been drawn from an analysis of available statistics on school population and cost of education. Obviously they cannot be considered as definitively proven. For example, there

is no factual evidence that the desire to give the offspring a higher education is causally related to contraceptive efforts. However, the general economic and labor problems that emerge from the increase in the size of secondary school population are of the highest importance and the authors have done well to bring them out into the open. It is hoped that the future will see a more intensive analysis of the question in this country.



A DOCTOR'S HOLIDAY IN IRAN.

By Rosalie S. Morton. Foreword by Hugh S. Cumming. Funk and Wagnalls, New York and London. \$3.00. 8¼ x 5½; xi + 335; 1940.

The awakening of the Near East, at a time when Europe is deeply engaged in mutilating her own more recent civilization, may possibly mean a surging upward of forces that have long been lying fallow. A great people and a great culture once flourished here. Would it not be possible for something of that greatness to return? Dr. Morton does not say this in so many words, but she is deeply impressed with the new social and national consciousness that is emerging in what is now Iran—and was so-called before the land was given the name of Persia. Through sheer ability the present Shah, Riza Pahlavi, has risen, like our own Lincoln, from poverty to become a great leader. As in Turkey, great changes are taking place in the lives of the people, but the task is far more difficult than in Turkey because of the greater isolation of Iran and its more burdensome traditions and customs. Nevertheless, the Shah is rebuilding a nation and giving his people self-confidence and self-control.

Dr. Morton, a keen observer, writes most interestingly of her travels throughout the land. Comparing the usefulness of the camel and the automobile, she is inclined to agree with one who told her

As an all-round investment nothing equals a camel, for when it is born it costs nothing, it finds its own food, wears far longer than an automobile, needs no repairs, can carry passengers and freight, is always reliable, goes well on rough roads and in the sand, needs no garage, gas or oil; receives water at conven-

ient times and places and uses it economically; when too old to work it becomes a religious sacrifice, after which its meat can be eaten. Its skin is useful for many purposes, its bones are used for jewelry, both carved and painted. In comparison, what value is an automobile? It cannot even reproduce itself!



JAMES GEORGE FRAZER: *The Portrait of a Scholar.*

By R. Angus Downie. Watts and Co., London. 5s. net. 8½ x 5½; ix + 141; 1940.

To those who have followed Sir James Frazer's writings this little volume, written by one who has been closely associated with the great anthropologist in recent years, will be of much interest. Downie herein gives a brief biographical sketch of Frazer, a survey of his work in the classical and anthropological fields, as well as his literary studies of modern times and writers, and concludes with an estimation of the influence which Frazer has had on human thought.

In 1888 Frazer wrote "Taboo" and "Totemism" for the *Encyclopaedia Britannica*. It was in the preparation of these articles that he began "a systematic application to anthropology and especially to a study of the backward races of men whom we call savages and barbarians." The *Golden Bough* originally appeared in two volumes in 1890. Later (1911-1915) it was revised and extended to the well-known 12 volumes, with a 13th volume *Aftermath* appearing in 1936. In 1898 appeared the 6 volume edition of Pausanias—Frazer's greatest work as a classical scholar. *Totemism and Exogamy* appeared in 1910, and *Folk-Lore in the Old Testament: Studies in Comparative Religion, Legend, and Law* in 1918. Frazer's many works have been written by his own hand "with no assistance beyond that of a steel pen."

The volume concludes with a short bibliography of Frazer's works (56 titles) and an index.



I REMEMBER. *The Autobiography of Abraham Flexner.*

By Abraham Flexner. Simon and Schuster,

New York. \$3.75. 9½ x 6½; xii + 414 + 17 plates; 1940.

It now seems difficult to realize that practically all the advances made in medical education in the United States have occurred since 1908, the year in which Abraham Flexner began, for the Carnegie Foundation for the Advancement of Teaching, his study of the status of and conditions in the medical schools in this country and in Europe. His report was the impetus to the development of the full-time medical school with raised entrance requirements and complete clinical and laboratory facilities—one school reported on in 1908 had a "physiological laboratory" consisting solely of one sphygmograph.

In this well-written autobiography Flexner gives a detailed, but not tiresome, account of his investigations into the state of medical schools, as well as of the methods, advanced for their time, employed in his fifteen-year career as teacher in his private school in Louisville, Kentucky, which preceded his connection with the Carnegie Foundation. Likewise he relates in a modest manner the part he played in the investigations conducted for the Carnegie and Rockefeller Foundations into the teaching in universities, colleges, high schools, and elementary schools in the United States, and the progress and changes of educational methods which followed throughout the country. The history of the Institute for Advanced Study which he founded at Princeton in 1930 and still directs, is also told.

This book is well indexed, and the whole constitutes an interesting and adequate history of modern education in the United States.



THE PREHISTORIC FOUNDATIONS OF EUROPE. *To the Mycenaean Age.*

By C. F. C. Hawkes. Methuen and Co., London. 21s. net. 8½ x 5½; xv + 414 + 12 plates + 6 maps and tables; 1940.

This book will delight the thoughtful reader. It presents a great mass of data on early European culture but in such an

orderly fashion that the reader soon realizes that here at last is unity between historic and pre-historic times. In other words, civilization of today can now, in many of its phases, be traced far, far back into pre-historic times. The author finds the whole story of human culture in Europe

indissolubly bound up with the physical character of Europe itself, the landscape and climate which have made the environment of human culture. And that character is unique.

The diversity of altitude and structure between its Alpine spine and the Mediterranean and Baltic depressions to the south and north give life and landscape a wide range of conditions for its relatively small size. In short, it is capable, under secular changes of land-form and climate, of forming a natural paradise for the play of *adaptive vitality* [our italics].

It is in adaptive vitality that the author finds grounded the moving pattern of European achievement. "The movement of the pattern, the instability of the balance, seem throughout characteristic of historic process in Europe, as against the 'changeless East', which invented civilization only to stagnate in it. . . ." "The instability of Europe's equilibrium has been not its weakness but its strength; . . ."

Twelve plates, 6 maps, tables, and many text figures add to the interest of the volume. Twelve pages of bibliographical notes follow the text and there is an excellent working index.



THE ANTHROPOLOGICAL JOURNAL OF THE INSTITUTE OF HISTORY AND PHILOLOGY. *Academia Sinica. Volume 1, Part 1.*

Edited by T. L. Woo, S. S. Ling and S. Y. Liang. The Commercial Press, Shanghai. 10½ x 7½; 233; 1938.

T. L. Woo contributes the first paper "An anthropometric study of the Chinese clavicle based on the Hsiao T'un and Hsiu Chiu Shan specimens" in this interesting new publication. Two series of clavicles (155 male and 95 female) from different regions of China and representing populations of the Sui-T'ang dynasties and of modern times were studied with respect to ten indices, for some of which new methods of measurement are devel-

oped. The right clavicles were found to be, on the average, shorter, stouter, and more curved than the left. A marked differentiation between the clavicles of the two sexes was revealed in average absolute measures but in the measurements of shape no marked sexual differences were found. This paper is in English. The following three articles, A study of the U-Man and Pei-Man of Yunnan in the T'ang dynasty, by S. S. Ling; On the divination of the Moso tribe in Yunnan, by Y. K. T'ao; and Miao stories of a great flood and the legends of Fu-hsi and Nü-wa, by Y. F. Ruey are in Chinese. The fifth study, in English, on the glabella prominence of the human cranium, is based on series of skulls from various parts of the world preserved in the Museum of the Institute of History and Philology (Chinese specimens) and the Museum of the Royal College of Surgeons, London. The racial types of cranium differed quite appreciably in both size and shape of glabella. New instruments for the measurement of hand and foot circumferences are described and illustrated in the closing article (in German) by T. L. Woo.



FAMILY INCOME AND EXPENDITURES. *Middle Atlantic and North Central Region and New England Region. Part 1, Family Income. U. S. Department of Agriculture. Miscellaneous Publication No. 370. Consumer Purchases Study. Urban and Village Series.*

By Day Monroe, Elizabeth Phelps and Idella G. Swisher. Government Printing Office, Washington. 50 cents. 9½ x 5½; iv + 446; 1940 (paper).

FAMILY INCOME AND EXPENDITURES: *Pacific Region and Plains and Mountain Region. Part 1, Family Income. U. S. Department of Agriculture. Miscellaneous Publication No. 356. Consumer Purchases Study. Farm Series.*

By Day Monroe, Dorothy S. Martin, Margaret Perry, and Kathryn Cronister. Government Printing Office, Washington. 30 cents. 9½ x 5½; iv + 276; 1939 (paper).

These two books refer specifically to the subject of family income. The first covers investigations in small cities and villages of the Middle Atlantic, North Central and New England Regions. The second contains the results of investigation of income of farm families of the Pacific Region, and Plains and Mountain Regions. The information obtained is presented mainly in statistical form, and is broken down into studies of family income from many different angles, dealing with income and earning capacity as related to age, sex, occupation, place of residence, home ownership, etc. These studies will be of use to economists, and to biologists investigating the subject of population.



POPULATION POLICIES AND MOVEMENTS IN EUROPE.

By D. V. Glass. Oxford University Press, New York; The Clarendon Press, Oxford. \$6.00. 8½ x 5½; vi + 490; 1940.

In this volume Glass presents a comprehensive review of a major proportion of the recent literature on population problems in an effort to clarify the two main questions with which students are concerned, to wit: the future trend of natality and the general effects of such a trend. The author reexamines first the decline in the natality of England and the factors which may have influenced it. The inferences that he draws follow the accepted pattern. He then proceeds to a survey of state intervention and compares the demographic policies of the Scandinavian countries, France, Belgium, Germany, and Italy. This survey comprises the greatest portion of the book and constitutes its most remarkable feature since the author has brought together the available information on the matter and discusses fully the underlying theories and practical applications of the governmental policies. The final conclusions reached by the author are, in essence, (a) that there is not sufficient knowledge to permit accurate predictions of the future trend in natality; (b) that the attempts to increase natality by state intervention have not been successful. With these conclusions everyone

will agree. The author also describes briefly in an appendix the methods of determining certain statistical constants useful for demographic studies. An ample bibliography is included and although omissions are to be noted this volume will be found useful as a source of reference to the latest reports on the subject.



PASCUA: A Yaqui Village in Arizona.

By Edward H. Spicer. University of Chicago Press, Chicago. \$3.50. 8½ x 5½; xxxi + 319 + 13 plates + 9 charts; 1940.

The village of Pascua is geographically part of the city of Tucson—culturally it is completely isolated from the dwellers about it. Linguistically the Yaqui Indians are not very closely related to those of Arizona, and they have had a widely different history. Whereas the native Arizona Indians are mostly pueblo dwellers and do not take kindly to Nordic civilization, the Yaquis adopted Spanish culture, and entered the United States only about half a century ago, as the result of persecution at the hands of the Diaz administration. They are not Mexicans, they are not "Saxon Americans," they are Indians, but of a widely different type from those about them.

Such a group of people (there are only about 2500 of them altogether, and less than 500 in Pascua) cannot but be of great interest to the student of sociology, and the author of this book has produced an excellent piece of work, covering all phases of the life of these people—their work, their play, their language, their religion, their education, what food they eat, how they conduct their ritual dances, their baptisms, and their funerals. There is a bibliography of two pages, an index of seven, and numerous photographs. It is an excellent study of an isolated cultural community, quite unlike anything else in the United States.



ESSAYS IN POLYNESIAN ETHNOLOGY.

By Robert W. Williamson. Edited by Ralph Piddington, with an analysis of

recent studies in Polynesian history by the Editor. The Macmillan Co., New York; The University Press, Cambridge. \$7.00. 9½ x 6½; xlii + 373 + 10 plates + 2 maps; 1939.

This handsome volume completes the final series of studies that Williamson had undertaken in the social anthropology of Central Polynesia. Three volumes have previously appeared on the following general topics: social and political systems; religious and cosmic beliefs; and religion and social organization. Much material, however, still remained to be recorded and the first five chapters of the present work embody these posthumous manuscripts. The chapter headings are as follows: Warfare in Central Polynesia; Kava in Samoa and Tonga; Kava in other Polynesian islands; The *Arioi*; Sex, courtship and infanticide. The main part of the volume (Part II) is a discussion of historical problems in Polynesia. It

represents an attempt to assess the present position of historical studies in Polynesia, with special reference to certain views which have been propounded since Williamson's death. It is concerned with certain recent theories of Polynesian origins and these have a bearing on the controversy between the historical and functional schools, a controversy which has reached a critical stage during the present decade, and which is unquestionably the most important issue in anthropology today.

Piddington contributes the preface to this scholarly work; a bibliography with abbreviations precedes the textual matter; a map, a number of plates and numerous footnotes occur in the text; and an appendix on Assam parallels and a detailed index conclude the volume.



BERKELEY MOYNIHAN, Surgeon.

By Donald Bateman. With a Preface by Lord Moynihan. The Macmillan Co., New York. \$4.00. 8½ x 5½; xv + 354 + 8 plates; 1940.

This interesting volume is an account of the life of the first Baron Moynihan of Leeds, one of the dominant figures in British surgery during the first three decades of this century. A man of high ideals, striking force of character, and exceptional charm of manner and mind, Moynihan had

the great honor of being the first provincial surgeon to be made President of the Royal College of Surgeons—an unwritten rule being that the President should be a member of the staff of a London teaching hospital. He remained, however, always loyal to Leeds and continued to do much of his practicing there.

Many physicians and surgeons in this country will remember Moynihan's speeches (he was a famous orator) when in the fall of 1917 he was assigned by the British Government to advise the U. S. Army Medical Corps in its preparations. His speeches fell into two classes: those of a strictly surgical interest, and those upon the general aspects of the war. These latter, before lay audiences for the purpose of advancing the allied cause, he delivered with great effect.

Bateman has included in the volume many interesting letters and a number of illustrations.



TODAY AND DESTINY: *Vital Excerpts from The Decline of the West of Oswald Spengler.*

Arranged with an Introduction and Commentary by Edwin F. Dakin. Based on the text of the Authorized Translation of Charles F. Atkinson. Alfred A. Knopf, New York. \$2.75. 8½ x 5½; viii + 364; 1940.

Spengler belonged to that very small group of social philosophers that does not subscribe to the prevalent view that every day in every way our civilization is proceeding to a higher and more sublime level. Moreover, he believed, as many others have, that political history proceeds in inevitable cycles. Twenty years ago he was so bold as to predict that the 19th century liberal form of government would gradually be displaced by dictatorship and all that this entails. These views never pleased the professional and orthodox sociologists who therefore made a point of demonstrating the technical and methodologic inadequacies of Spengler's work. Dakin, who apparently has read Spengler carefully, protests against the injustice done him and particularly against the label of Nazi which has been attached to him. To indicate the objec-

tives of Spengler's study Dakin has brought together in this volume excerpts from the famous *The Decline of the West*. It is the editor's intention to show that Spengler deplored the end of democracy and was really attempting to awaken the people to the need for defending it. Dakin seeks to do the same now by reiterating Spengler's words.



ORDER AND POSSIBILITY IN SOCIAL LIFE.

By Douglas G. Haring and Mary E. Johnson. Richard R. Smith, New York. \$4.00. 9½ x 6; xii + 772; 1940.

This textbook on sociology takes its title from an essay by the late F. H. Giddings to whom the book is dedicated. The subject matter is arranged under five main headings. In the first part, certain aspects of the social behavior of several peoples not of western civilization are described. The second and third parts deal summarily with evolution, heredity, and the physiological and psychological manifestations of man. Books four and five touch on the formation of societies and their varieties. This work has two distinctive characteristics. The first is that the authors have had recourse to extensive citations from the authorities in the fields covered. The second is that an attempt has been made to introduce into the picture of human social behavior its biological foundations. The attempt has not been completely successful because a net separation between social action and biological attributes is still noticeable. However, the authors have definitely progressed further along the objectives of human biology than most sociologists have and this volume is a good presentation of the essentials of the subject. It is to be deplored that the book lacks a list of references or some selected bibliography.



CULTURE AND SURVIVAL.

By Guy Chapman. Jonathan Cape, London. 8s. 6d. net. 8 x 5½; 243; 1940.

The general purpose of this book is "to discuss a single aspect of the growth and

decline of population in England and Wales, and more particularly the problem of the decline which today threatens. The aspect studied is the connection between what may be called culture, and the family." In the course of a survey of the changes in the nature of consumption goods over some centuries, the author was impressed with the rise in the standard of living and the decline in fertility; with the breaking up of rural culture and the development of leisure activities in the large cities. He shows how labor and capital have become more and more engaged in the production of goods for minor comforts such as labor-saving devices and amusements for the leisure hours of those who, only recently having acquired leisure, have no stabilizing background for the use of such freedom. This makes for a dangerous situation when the country must be put to the task of producing goods for war purposes. In the final chapter, "The Dilemma," he compares the industrial society and the changes in the birth rate of Germany with those of England.

Bibliographic footnotes are given throughout the text but the volume is not indexed.



YOUR LIFE IS THEIR TOY. *Rackets—Social Service and Medical.*

By Emanuel M. Josephson. Chedney Press, New York. \$3.50. 9½ x 6½; [12] + 449; 1940.

Josephson divides his "expose" into two parts—the social service rackets and the medical rackets. The author uses the word "racket" in the colloquial sense, in all of its shades of connotation, and as he proceeds there are few agencies and philanthropies which escape castigation. Josephson believes that every age has had its charlatans, quacks and medicine men and that the present period has produced a bumper crop which is exploiting mankind unmercifully. He further thinks that the consequence of this welter of exploitation is the sacrifice of human comfort, happiness, health, and life. The author states that his motive in presenting this treatise is not malice, but

rather the desire "to protect the health and life of the public and to see justice done." The book is well documented and presents a most challenging and provocative discussion of various aspects of modern society. A good index is appended to the volume.



THE NEW NOAH'S ARK.

By André Demaison. Translated by Eric Sutton. The Macmillan Co., New York. \$2.50. 8 x 5½; [10] + 294; 1940.

Sailing along the coast of Africa in an old schooner Demaison made a temporary business of collecting wild animals. The pages of his book are filled with the color of the sea and jungle. He describes the superstitions and prejudices of his half-caste crew and of the native tribes that he met along the way. But particularly interesting are the accounts of the behavior of the beasts. Yet the book is purely an adventure story and sheds no new light on the enigma as to how much of the intelligence of animals is due to actual thought and how much to instinct or response to physiological processes. The ordinary course of the voyage was punctuated by such unexpected events as the breaking loose of the water buffalo, the accidental arrival in a port rife with yellow fever, and as a climax, the poisoning of the crew, shipwreck, and escape with the precious cargo.



ESSAYS IN HISTORICAL ANTHROPOLOGY OF NORTH AMERICA. Published in Honor of John R. Swanton in Celebration of His Fortieth Year with the Smithsonian Institution. Smithsonian Miscellaneous Collections, Volume 100 (Whole Volume).

The Smithsonian Institution, Washington, D. C. \$2.00. 9½ x 6; [6] + 600 + 16 plates + 1 folding map; 1940 (paper).

Thirteen anthropologists, most of whom are ethnologists, have contributed to this volume which honors John R. Swanton. Kroeber introduces the work with an evaluation of Swanton's contribution to the knowledge and methodology of eth-

nological investigations. The articles, as the title indicates, are concerned with North American primitive peoples. The continent is effectively if not completely covered since the papers deal, respectively, with the peoples of Virginia and the Southeast, the Northeast, and of the northern Mississippi Valley, of the central and northern great plains, the Southwest, the great basin area, and the subarctic regions. It may be said that each paper represents a scholarly piece of work and this volume constitutes a survey of existing information on the subject.



IN SEARCH OF COMPLICATIONS. An Autobiography.

By Eugene de Savitsch. Foreword by Arthur Krock. Simon and Schuster, New York. \$3.00. 9½ x 6; [6] + 396; 1940. de Savitsch is still a young man, being about 37 years old, but he has already gone through more experiences than are usually acquired in a whole life time. Born in the higher Russian bourgeoisie, he fled at 14 from the Bolsheviks. He became for a short time an officer in the ill-fated White Russian army and then via Japan he migrated to this country. Here he was a floor-walker in a department store, nearly starved himself and contracted tuberculosis. When he recovered he turned to medicine for some reason and finally obtained a medical degree from Chicago University after a stopover at Colorado. These and other adventures are told with the style of a seasoned raconteur and patently aimed at bringing out the humor of the situations. As a result the book is interesting and amusing except in those very rare occasions when the author becomes pontifical about scientific matters.



CHINA'S ANIMAL FRONTIER.

By Clifford H. Pope. The Viking Press, New York. \$2.50. 9 x 6; 192; 1940. Everybody knows about Roy Chapman Andrews and some of the things he obtained from the desert of Central Asia.

But the story of the expedition itself is not so well known. In this work Clifford Pope, a member of the party, tells this story, and brings to life before the readers' eyes the various members of the expeditionary force, mostly Chinese, who officiated as artists, preparators, interpreters, cooks, etc.

The book is well illustrated and makes delightful reading. It should appeal to everybody. Although it contains much scientific matter, such as the discussion of alligators and dolphins, it is not primarily a scientific treatise but an adventure story.



RURAL POPULATION DENSITY IN THE SOUTHERN APPALACHIANS. *United States Department of Agriculture: Miscellaneous Publication No. 367.*

By Francis J. Marschner. *United States Department of Agriculture, Washington, D. C.* 25 cents. $9\frac{1}{2} \times 5\frac{3}{4}$; 18 + 1 folding map in pocket; 1940 (paper).

In general the population density of the Southern Appalachian region conforms to the rule that man will congregate in locations where the land is most productive. However, the present report shows that this relationship is not consistent, being complicated by numerous social and economic factors, and others the nature of which are less readily understood. No attempt is made to interpret these interrelationships, so the report is largely a factual presentation. It is accompanied by an excellent large population map of the area.



ZOOLOGY

PRINCIPLES OF ANIMAL BIOLOGY.

By Lancelot Hogben. *Illustrations by J. F. Horrabin.* W. W. Norton and Co., New York. \$3.75. $8 \times 5\frac{1}{2}$; 415; 1940.

In this work Hogben has sought to achieve two ends—to write a practical textbook of elementary biology for use in schools and colleges, and to write a popular treatise that would hold the interest of the reader who has but little technical knowledge, and from which he

might derive both pleasure and profit. Since these ends obviously could not be achieved simultaneously the book is divided into two parts. The first of these is built up around descriptions and discussions of the physiology and reproduction of the frog, though the other animals are by no means neglected. Each chapter is supplemented by a list of questions and subjects for home study.

The second part gives the author an opportunity to demonstrate his mastery of the art of self expression in writing. Beginning with the well-known passage from Gerard's *Herball* of 1594 dealing with the development of the barnacle goose (the original illustration from the *Herball* is reproduced) the author goes on to a discussion of the taxonomic systems of Linné, Cuvier, Lamarck, Leuckart, and Milne-Edwards, explaining not only how these systems differ, but also why.

The critical reader is apt to feel that this historical approach might have been reinforced by the inclusion of Aristotle, but the fact is that the author seems not very kindly disposed toward that worthy. To Aristotle he attributes responsibility for the parasitic growth of superstition that clouded the proto-science of the dark ages and impeded its progress, just as the progress of a ship is impeded by the barnacles on its bottom.

The work is supplemented by four appendices, a ten page index, and numerous excellent illustrations.



AN INTRODUCTION TO ENTOMOLOGY. *Ninth Edition Revised.*

By John Henry Comstock. *Comstock Publishing Co., Ithaca, N. Y.* \$5.00. 9×6 ; xix + 1064; 1940.

To students of entomology the name of Comstock has been both familiar and authoritative since 1888 when the author published his first *Introduction to Entomology*. During the early '90's this first work was replaced by *A Manual for the Study of Insects*, which in turn was later (1924) replaced by the first edition of the present text under the title of *An Introduction to Entomology*. The present edition (9th) under the editorship of

Glenn W. Herrick maintains the same high standard of workmanship responsible for the popularity of the earlier editions.

The material of the text is presented under two heads; (1) The structure and metamorphosis of insects; and (2) The classification and life histories of insects. In the former section are discussed such pertinent topics as the characteristics of insects and their nearest relatives, the external and internal anatomy of insects, and the factors relative to the metamorphosis of insects. The later section presents not only the keys for the classification of the 26 orders of insects, but also a short description of the adult, eggs, and immature stages of each insect, a discussion of the sex and seasonal variation in the color, form and activity of each form, as well as the distribution, feeding and breeding habits of the various species.

The text is amply supplied with illustrative material and is concluded with a bibliography of 521 titles and a detailed index.



INSECT TRANSMISSION OF PLANT DISEASES.

By Julian G. Leach. McGraw-Hill Book Co., New York and London. \$6.00. 9 x 6; xviii + 615; 1940.

One has only to glance at the appendix of this pioneering textbook to realize how many insects have been found to be vectors of plant pathogens. That tobacco mosaic is a plant disease nearly everyone must know, but that it is insect transmitted is uncommon knowledge. Proof of the rôle that insects play in the spread and development of plant diseases has accumulated rapidly since Waite, in 1891, made it evident that the bacillus of blight is carried from flower to flower by the honeybee. The author of the present volume became absorbed in this new field of study in 1923, when an investigation of the blackleg disease of potatoes led him to study the rôle of flies in the transmission of bacterial soft rot generally. Leach's work, first at the University of Minnesota and now at the University of West Virginia, led the late Dr. Royal N. Chapman to suggest that he write a book

to signalize the emergence of this new field of research. Here is the book. It is not intended to be an exhaustive treatise, yet it runs to 17 well-organized chapters, each with its list of references. The text is copiously illustrated. Like other works which are the first in their fields, this book promises to become a classic.



A GENERAL ZOOLOGY OF THE INVERTEBRATES.

By G. S. Carter. Foreword by Julian S. Huxley. The Macmillan Co., New York. \$5.50. 8½ x 5½; xxviii + 509; 1940.

As a rule books on invertebrate zoology go into the details of morphology and present only a brief discussion of the general biological problems involved in the process of living in a particular environment. It is the purpose of this book to discuss more completely these biological principles. Hence it is not a text-book of descriptive zoology, but is designed as supplementary reading to broaden the scope of the student, particularly in invertebrate physiology and ecology.

There are four sections in the volume, the first of which describes the fundamental physical, chemical, and biological properties of living cells. The second section discusses the problems of differentiation, growth, regeneration, form, and organization in the multicellular body. Next treated is the comparative physiology of the metabolic processes and of sensory response. The final section is devoted to the general problems of the life cycle, behavior, habits, and evolution of invertebrates. Some biologists may differ with the author in the details of certain opinions which he expresses, but on the whole the book is well written and logically presented. It contains a good index and a bibliography by topics.



THE BIRDS OF BUCKEYE LAKE, OHIO. *Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 44.*

By Milton B. Trautman. University of

Michigan Press, Ann Arbor. \$2.50. 10 x 6½; 466; 1940 (paper).

This survey sets a fine standard, and shows what can be done in an intensive study of the avifauna in a small area. The main part of the work was done by the author, but many others contributed to the study which was made over a twelve-year period. An attempt is made to give as complete a conception of the status of each bird species in the Buckeye Lake area (in the vicinity of Columbus) throughout historic times as is possible with the data at hand. This includes a brief account of the interglacial and postglacial history of the Buckeye Lake area, from Wisconsin time to the beginning of historic time; a brief discussion of the invasion and occupation of the area by the white man, and his influence and effect upon the topography, flora, and fauna, especially as regards birds; and a compilation of the literature concerning the bird fauna, and of unpublished data on it and on conditions in the area before February 1, 1922. Thereafter, the results of twelve years of bird observations made between February 1, 1922, and February 1, 1934, are given. Citations of literature, photographs and indexes of common and scientific names of plants and animals conclude the volume.



ZOOLOGICA. *Scientific Contributions of the New York Zoological Society. Volume XXV, Part 2, Numbers 11-18.*

New York Zoological Society, Zoological Park, New York. \$2.00. 10½ x 7; 163; 1940 (paper).

The following papers are contained in this number: Plankton of the Bermuda Oceanographic Expeditions. IX. The Bathypelagic Caridean Crustacea, by Fenner A. Chace, Jr. (64 text-figures); Eastern Pacific Expeditions of the New York Zoological Society. XIX. Actiniaria from the Gulf of California, by Oskar Carlgren (8 text-figures); Morphological and embryological studies on two species of marine catfish, *Bagre marinus* and *Galeichthys felis*, by Daniel Merriman (5 plates; 9 text-

figures); Propagation of the electric impulse along the organs of the electric eel, *Electrophorus electricus* (Linnaeus), by C. W. Coates, R. T. Cox, W. A. Rosenblith and M. Vertner Brown (1 plate; 3 text-figures); Notes on the display forms of Wahne's Six-plumed Bird of Paradise, by Lee S. Crandall (3 text-figures); Acute hemorrhagic gastro-enteritis in a giant panda, by Leonard J. Goss; Two new species of trematodes from the deep sea scorpion fish, *Scorpaena madurensis* Cuv. and Val., by Ross F. Nigrelli (1 plate; 2 text-figures); Report of the Hospital and Laboratory of the New York Zoological Park, 1939. Mortality statistics of the Society's collection, by Leonard J. Goss.



THE RABBITS OF CALIFORNIA. *Occasional Papers of the California Academy of Sciences No. XIX.*

By Robert T. Orr. California Academy of Sciences, San Francisco. \$3.50. 9½ x 6½; 227; 1940 (paper).

There is a wealth of material dealing with speciation and distribution of rabbits but very little about their habits and life histories. In view of this, the author has devoted over 150 pages of the volume to the life histories, habitats, behavior, food, reproduction, and natural enemies of the seven species, with their subspecies, which are found in California. In addition there are the more usual accounts of specific diagnosis, coloration, distribution, and measurements. The early pages include an account of the techniques employed in the investigation and a discussion of the possible origin of geographic variation. Since the latter is the only section involving speculation, it is the most open to disagreement, particularly by students of evolution and heredity. The author finds that a negative correlation exists between degree of variation and the ability of dispersal, but the reason for the correlation is subject to question. There are several pages of bibliography and numerous photographs.

INTIMATE SKETCHES FROM BIRD LIFE.

By Eric Hosking and Cyril W. Newberry.
 With an Introduction by Julian S. Huxley.
 Country Life, Ltd., London. 5s. $8\frac{1}{2}$ x $5\frac{1}{2}$; xx + 104 + 53 plates; 1940.

In this fascinating little book Hosking and Newberry have recorded a number of pertinent observations of bird life in the field. In support of the discussions of various phases of the life and activities of some eight species of English birds are a number of excellent photographs.

The authors have included in their discussions the methods of constructing blinds, the procedures for making careful field observations, and the techniques necessary for successful bird photography. The material of the book is for the most part a record of field observations and objective data, though there are occasional minor excursions into the theoretical with regards to the evolution, the intelligence, and the emotions of birds.

For all nature lovers, particularly those interested in ornithology, the book is well worth the reading time.



AN OUTLINE OF GENERAL ZOOLOGY.

By Gordon Alexander. Barnes and Noble, New York. \$1.00. $8\frac{1}{2}$ x $5\frac{1}{2}$; [16] + 280; 1940 (paper).

This is another of the popular college outline series and bids fair to rival the success of the other members of this group of publications. The volume is in four parts: Principles of organization of the animal body, Survey of the animal kingdom, Biological principles, and an Historical summary. This outline is designed to be used as a supplement to standard textbooks used in either of the two kinds of college courses in zoology—the so-called survey and principle courses. The outline may also be used as a syllabus or condensed textbook in courses with a complete lecture plan. The numerous illustrations are well-chosen. The appendix includes an abridged classification of animals and a glossary of important terms. The book is indexed.

ABOUT SPIDERS: *Introducing Arachne.*

By Elaine V. Emans. Drawings by Viola A. Young. Photographs by Lee Passmore and O. C. Kuehn. E. P. Dutton and Co., New York. \$2.50. 8 x $5\frac{1}{2}$; 183 + 11 plates; 1940.

Not to be too harsh with the writer of this book it must be said that the amateur biologist may gather from its pages many of the facts of spider life. These include home-building, reproduction, the economic importance of the arachnids, and other bits of interest such as that "though probably no cracker has ever been patterned after it, the spider is a little animal, and not an insect." Miss Emans reaches the pinnacle of simplicity and imagination in biological writings. *About Spiders* is an excellent story for children. An effort is made to dispel prejudice against spiders by treating them as household pets whose names are "Beautiful Lady," "Silver Queen," and "Brave One."



AN ATLAS OF THE FROG.

By Paul L. Carroll and Wilfred F. Horner. C. B. Mosby Co., St. Louis. \$1.25. $10\frac{1}{2}$ x $7\frac{1}{2}$; 109; 1940 (paper).

The popularity of the frog as a typical vertebrate for college study has brought into print an abundance of work books, syllabi, and atlases on this common amphibian. The present atlas follows closely the general run of these. It includes labelled drawings of the skeletal, musculature, digestive, respiratory, urogenital, circulatory, and nervous systems.

The loose-leaf form of the atlas conforms to the recent trend in providing the student with a clear, precise and simplified laboratory manual. For college classes that require spoon-feeding in their general biology courses, this atlas should furnish at least part of their pre-digested gruel.



ANIMALS IN ACTION.

By Gayle Pickwell. Whittlesey House, McGraw-Hill Book Co., New York and

London. \$4.00. 11 $\frac{3}{4}$ x 8 $\frac{3}{4}$; xii + 190; 1940.

Each book put out by this author seems to be more fascinating than the preceding one. In this beautiful volume are described and illustrated many interesting phases in the lives of animals—the getting of food, locomotion, protection, breathing, etc. Being a master of photography as well as a careful student of nature the author has produced a work that should stimulate many a young naturalist to follow in his footsteps.



A REVISION OF THE NORTH AMERICAN APHIDS OF THE GENUS MYZUS. *United States Department of Agriculture Miscellaneous Publication No. 371.*

By Preston W. Mason. *United States Department of Agriculture, Washington, D. C.* 5 cents. 9 $\frac{1}{8}$ x 5 $\frac{1}{2}$; 30; 1940 (paper).

Listed here are 20 species (3 of which are described as new) of the genus *Myzus* Passerini, together with their primary and secondary host, their distribution, their natural history and their economic importance. There is a detailed description of the seasonal variants of each group, a key to the identification of *Myzus*, and many helpful drawings. A bibliography of 35 titles and an index conclude this 30-page bulletin.



TRANSACTIONS OF THE SAN DIEGO SOCIETY OF NATURAL HISTORY, Vol. 9, Nos. 21, 22, 23 and 24. *A New Cardinal from Central Lower California, Mexico*, by Laurence M. Huey; *A New Form of Pocket Gopher (Thomomys) from the Santa Cruz Mountains, California*, by Laurence M. Huey; *A New Coastal Form of Brush Rabbit from the Vicinity of San Quintin, Lower California, Mexico*, by Laurence M. Huey; *A New Species of Legless Lizard from San Geronimo Island, Lower California, Mexico*, by Charles E. Shaw.

Society of Natural History, San Diego, Calif. 10 $\frac{1}{2}$ x 6 $\frac{1}{4}$; No. 21, 4; No. 22, 2; No. 23, 4; No. 24, 4; 1940 (paper).

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY. Vol. 42, Nos. 8, 9, 10. *The Pinyon Mouse (Peromyscus truei) in Nevada, with description of a new subspecies*, by E. Raymond Hall and Donald F. Hoffmeister; *Geographic Variation in Bushy-tailed Wood Rat*, by Emmet T. Hooper; *A New Race of Salamander, Ensatina eschscholtzii picta, from Northern California and Southern Oregon*, by Wallace F. Wood. *University of California Press, Berkeley and Los Angeles.* 25 cents each. 10 $\frac{1}{4}$ x 6 $\frac{3}{4}$; No. 8, 5; No. 9, 18; No. 10, 3; 1940 (paper).



BOTANY

TEXTBOOK OF GENERAL HORTICULTURE.

By Julian C. Schillester and Harry W. Richey. *McGraw-Hill Book Company, New York and London.* \$5.00. 9 x 6; ix + 367; 1940.

The urgent need in American agricultural colleges for a textbook in general horticulture has furnished the stimulus for preparing this excellent volume. The authors have been aware of the fact that it is practically impossible to organize a general course in horticulture which could be readily used by all types of classes in all regions of the United States, and in consequence, have planned this text around the general concepts and broad principles of the subject, rather than around the specific practices and techniques which vary from place to place throughout the country.

The early chapters of the book deal with horticulture in relation to man's industry, economy, and social well-being throughout the world. There follow several chapters on the structure, function and physiological processes of the horticultural plants, as well as their relation to the environment. The importance of soil management, and the care required for correct propagation, pruning, and training of plants are stressed. The volume closes with several chapters on the control of insect pests and the harvesting and storing of horticultural products.

From this body of well chosen and clearly presented material, it is obvious

that the requirements for different types of classes can be filled. The text will certainly be welcomed in its field.

The inclusion of numerous helpful illustrations, review questions, problems, and suggested collateral reading in each chapter, as well as the detailed index add to the excellence of this fine book.



ELEMENTS OF BOTANY. *Third Edition.*

By Richard M. Holman and Wilfred W. Robbins. John Wiley and Sons, New York; Chapman and Hall, London. \$2.75. 9 x 5½; xi + 392; 1940.

This abridged text is designed especially for use in institutions in which only one semester is devoted to general botany, or in which the subject is less extensively studied than usual. The first part of the book deals with the structure and physiology of seed-bearing plants, and in the second part the various phyla of the plant kingdom are discussed in order. Considerable attention has been given in this new edition to applications and items of general interest. Mention is made at logical places of such topics as the role of growth substances and their use in agricultural practice, water-culture methods of growing plants, root systems in relation to soil erosion, methods used in altering the duration of the life cycle of plants, artificial pollination, self-sterility in commercial fruit varieties, economic importance of plant diseases, control of weeds, "hardening" of plants, "short-day" and "long-day" plants, economic value of certain plants and of various plant products, and methods employed to induce chromosome changes. The book is well illustrated. There is no bibliography, but a good index is provided.



FOREST OUTINGS.

By Thirty Foresters. Edited by Russell Lord. United States Department of Agriculture, Washington, D. C. \$1.25 (cloth); 75 cents (paper). 10½ x 7½; xiv + 311; 1940.

The pleasures, romances, and healthful

modes of recreation that our national forest parks offer are here recounted in a most interesting fashion by 30 foresters. There is also an account of the administration of our 161 "monuments to nature" in an attempt to make and keep them as "zoos without cages." The discussions deal with such diversified subjects as camps, winter and summer sports, dangers from fires and floods, and the conservation of timber, soil, and wild life. The generous supply of excellent photographs are enticing bait to lure the reader into the more worthwhile things in the text.

A short bibliography, a note on the basic principles governing the recreational management of the national forests, a map and several tables indicating the location and size of the national parks, a table of the big game census of the national forests as of January 1, 1939, and an index complete the volume.



BOTANY OF THE MAYA AREA. *Miscellaneous Papers XIV-XXI. Publication 522.*

Carnegie Institution of Washington, Washington, D. C. \$2.75 (cloth); \$2.25 (paper). 10 x 6½; [4] + 474 + 7 plates; 1940.

This comprehensive survey of the vegetation in the Maya region, involving extensive systematic studies, contains the following papers: The 1936 Michigan-Carnegie Botanical Expedition to British Honduras (four plates and one map), by C. L. Lundell; The apocynaceous flora of the Yucatan Peninsula (six text figures), by R. E. Woodson, Jr.; The Bromeliaceae of the Yucatan Peninsula (twenty text figures), by L. B. Smith and C. L. Lundell; The Eriocaulaceae, Verbenaceae, and Avicenniaceae of the Yucatan Peninsula, by H. N. Moldenke; The Labiatae of the Yucatan Peninsula, by Carl Epling; The sedges of the Yucatan Peninsula (three text figures), by Hugh T. O'Neill; The Melastomaceae of the Yucatan Peninsula, by H. A. Gleason; The Bignoniaceae of the Maya area (three plates), by R. J. Seibert. The subject matter is presented in great detail, each paper concludes with an index to cited specimens and at the end

of the volume is an index to publications 461 to 522 in this series.



PHYSIOLOGICAL STUDIES OF JERUSALEM-ARTICHOKE TUBERS *with Special Reference to the Rest Period.* United States Department of Agriculture: Technical Bulletin No. 657.

By Clarence E. Steinbauer. United States Department of Agriculture, Washington, D. C. 15 cents. 9½ x 5½; 52; 1939 (paper).

The importance of the Jerusalem-artichoke (*Helianthus tuberosus* L.) as a possible source of levulose and of food for diabetics has been realized only in the past few years. In this bulletin, the author has recorded an enormous quantity of data concerning the chemical analysis of the Jerusalem-artichoke tubers both in the growing and resting stages. The study includes also the effects of different temperatures and chemical treatments in storage on the length of the resting period and the time required for sprouting. A storage temperature of 32° C. seems to be conducive to the shortest rest period and the best sprouting. None of the chemicals used produced any noticeable effect on speed of sprouting.

The paper includes an extensive review of the literature, as well as numerous photographs, charts and tables.



TREES.

By Samuel R. Stevens. Cecil Baugh and Company, Dallas, Texas. \$3.00. 9 x 6; xiii + 201; 1940.

The value of trees in the complex economy of man's life is the central theme of this intriguing little book. Supporting this theme are such topics as the history of the saw and sawmilling, sign language used in sawmills, lumber grading, the process of drying and the shrinkage of lumber, conservation and reforestation, as well as a discussion of many famous trees in history. Throughout the text there is a plea for the conservation of trees and for a more thorough program of reforestation, not only for industrial

purposes, but simply for the beauty and the grandeur of the tree as such. Scientific readers will be annoyed by the author's constant use of the word "specie" when describing a single species.

The book is well illustrated and documented, but there is no index.



FLORA HAWAIIENSIS. *The New Illustrated Flora of the Hawaiian Islands.* Book 4.

By Otto Degener. (Obtainable from the author, Waiialua, Oahu, Hawaii). \$3.50. 9½ x 6½; 330; 1940.

This is Book 4 of a comprehensive work that is being published at irregular intervals in loose-leaf fascicles (Centuries), each book containing 100 descriptions and 100 full-page illustrations. The arrangement is such that as each new book appears the pages can be taken out and placed with the old in taxonomic sequence. The *Flora* is planned for the student and nature-lover but it will be found a useful guide by Hawaiian visitors who are interested in the luxuriant vegetation of the islands.



FUNDAMENTALS OF BACTERIOLOGY. *Second Edition, Revised.*

By Martin Frobisher, Jr. W. B. Saunders Co., Philadelphia and London. \$4.00. 7½ x 5½; xvii + 653; 1940.

The second edition of this text is welcome (for mention of first edition cf. Vol. 12, p. 373). The author has revised his book with the idea in mind "that there is no longer any reason . . . to regard bacteriology as an exclusively medical science." This could well be a starting-point for a consideration of the fundamentals of any biological science. History, principles, technique, mode of action, and the industrial and medical aspects of microbiology are discussed.



ELEMENTARY BACTERIOLOGY. *Fourth Edition, Revised.*

By Joseph E. Greaves and Esthelyn O.

Greaves. W. B. Saunders Co., Philadelphia and London. \$3.50. 7 $\frac{1}{2}$ x 5 $\frac{1}{2}$; xiv + 587; 1940.

This is the fourth edition of a textbook for an introductory course in bacteriology. The previous editions as they appeared have been reviewed in the Q.R.B. The material is presented in a style such that the person whose chief qualification for admission to the course is his interest in the world around him, will find his way to a better understanding of disease and its control. The many illustrations are helpful.



APPLIED MYCOLOGY AND BACTERIOLOGY.

By L. D. Galloway and R. Burgess. Chemical Publishing Co., New York. \$4.00. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; viii + 186; 1940.

This edition brings up to date a book first published in 1937. New material and illustrations have been added, and the bibliography has been expanded to include recent literature. As before, the emphasis is on the economic value of microbiological techniques.



MORPHOLOGY

THE ENAMEL OF HUMAN TEETH: *An Inquiry Into the Formation of Normal and Hypoplastic Enamel Matrix and Its Calcification.*

By Moses Diamond and Joseph P. Weinmann. Columbia University Press, New York. \$1.50. 10 $\frac{3}{4}$ x 7 $\frac{1}{2}$; viii + 105; 1940 (paper).

Retzius's concept that human tooth enamel is formed from within outward and that the organic matrix is calcified progressively as developed has been generally accepted during the past century. The present authors here show that this concept must be expanded. They separate the development of tooth enamel into two processes—the formation stage "during which the adult thickness of enamel is formed in a matrix state with calcium salts contained therein, probably in colloidal form," and the calcification state "which is regarded as a crystalliza-

tion phenomenon of the colloidal calcium." Their evidence is based on chemical studies and photomicrographs of enamel matrix formation. Hypoplasia and tooth injuries are treated to some extent but the conclusions with respect to these seem to be based on too little evidence. This book is profusely illustrated, and there is a bibliography of 36 titles.



PHYSIOLOGY AND PATHOLOGY

MEDICAL WORK OF THE KNIGHTS HOSPITALERS OF SAINT JOHN OF JERUSALEM.

By Edgar Erskine Hume. Foreword by His Most Eminent Highness Fra Ludovico Chigi-Albani. Preface by Lieut.-General Sir Aldo Castellani. The Johns Hopkins Press, Baltimore. \$3.00. 10 x 7; xxii + 371; 1940.

This is the first comprehensive account in English of the accomplishments of that remarkable organization, the Knights Hospitallers of Saint John of Jerusalem. The author has performed his task with meticulous care. Having a knowledge of languages he has been able to comb many sources for his material and the result is an accurate and most interesting story of the medical and charitable work of the Order and its historical background.

Three periods are given: (1) from the foundation of the Order in Jerusalem in the latter half of the 11th century, and the establishment of other hospitals throughout Christendom, to the occupation of the island of Malta in 1530; (2) the period of occupation of Malta (1530-1798); (3) from the loss of Malta to the present (1798-1940). From the very early times there were Sisters of the Order as well as Knights, and both sexes (Mohammedans, Jews, and Christians alike) were received as patients, including abandoned infants. Of much interest are the rules and regulations concerning sanitary arrangements, food, and behavior (of both patients and nurses). Of the size of the first hospital to be established, a visitor to Jerusalem prior to 1187 writes:

Here on the south side of the church, stands the Church and Hospital of St. John the Baptist. As for

this, no one can credibly tell another how beautiful its buildings are, how abundantly it is supplied with rooms and beds and other material for the use of poor and sick people, how rich it is in the means of refreshing the poor, and how devotedly it labors to maintain the needy, unless he has had the opportunity of seeing it with his own eyes. Indeed, we passed through this palace, and were unable by any means to discover the number of sick people lying there; but we saw that the beds numbered more than one thousand.

The volume is beautifully printed and illustrated and concludes with a list of references and a carefully planned index.



THE CHINESE WAY IN MEDICINE.

By Edward H. Hume. *The Johns Hopkins Press, Baltimore.* \$2.25. 7½ x 5½; [8] + 189; 1940.

This book tells in a clear-cut way the story of Chinese medicine from earliest records on through the centuries. Reduced to fundamentals, Chinese medical practice depended for centuries largely on the effect of mind on matter, and this enemy of disease having been exploited to the fullest extent, nature was then called in to do the rest. The Chinese did, however, resort early to the use of herbs, animal products, and minerals in the treatment of disease, and many of these are now of recognized value by the medical profession throughout the world. Hua T'o, in the second century, discovered the use of anaesthetics and became skillful as a surgeon. He gave his patients

an effervescent powder in wine which produced such numbness and insensibility that he could open abdomen or back, as the case might be, and wash, cut, or remove diseased organs. He would apply sutures, then cover wounds with a salve, and count on their healing completely in four or five days, the tissues returning to normal within a month.

The *Pulse Classic*, in ten volumes, one of the standard works in clinical medicine, was written in the third century. Hume says that proficient Chinese physicians of the old school show an almost uncanny power in diagnosing organic diseases by pulse observations alone. But it is only after years of experience that this art is acquired, the procedures being far more complicated than merely noting the rate, the volume, and the tension.

The volume is thoroughly documented and there is an index.



СТАРОСТЬ (Труды Конференции по Проблеме Генева Старости и Профилактики Преждевременного Старения Организма). Киев, 17-19 Декабря 1938 г.

А. А. Богомолец, Редактор. Издательство Академии Наук УССР, Киев. 245 x 163; 492; 1939.

[OLD AGE. (*Proceedings of the Conference of the Problem of the Development of Old Age and the Prevention of Premature Aging of the Organism*), Kiev, December 17-19, 1938.

Edited by A. A. Bogomolets. Publishing Agency of the Ukrainian Academy of Science, Kiev. 9½ x 6½; 490; 1939.]

The Conference of the Problem of the Development of Old Age and the Prevention of Premature Aging of the Organism was a joint enterprise set up by the Institute of Clinical Physiology of the Ukrainian Academy of Science, the Institute of Experimental Biology and Pathology of the Commissariat of Public Health, and the Institute of Clinical Medicine of the Commissariat of Public Health, all of the Ukrainian Soviet Socialist Republic. The thirty-nine papers presented at the meetings are published in this volume. Many of these are based on experimental material on physiological and biochemical processes and changes in old age. S. Tomeline has contributed a paper on the statistics of persons over sixty in various countries. French summaries have been provided. The bibliography is divided into the following divisions: works in the Russian and Ukrainian languages and translations from these (171 items); books and monographs in languages other than Russian or Ukrainian (117 titles); publications in periodicals other than Russian or Ukrainian, subdivided by subject (738 titles).



RHEUMATIC FEVER. *Studies of the Epidemiology, Manifestations, Diagnosis, and Treatment of the Disease during the First Three Decades.*

By May G. Wilson. *Commonwealth Fund, New York; Humpbrey Milford, London.* \$4.50. 10 x 6½; xiv + 595; 1940.

Rheumatic fever, under which title are included acute polyarthritis, chorea, and rheumatic carditis, still remains today one of the most obscure diseases or syndromes. As a clinical entity its boundaries are not very well defined, its etiology is unknown and the part played by contagion and by heredity in its transmission is controversial. The author has devoted considerable time to the investigation of these questions and in this volume summarizes her clinical and research experience as well as the more recent observations reported by others. In the first of five parts the epidemiology and etiology of the disease are discussed. The second part concerns the clinical and pathological manifestations of the disease, the third is devoted to its course in the first three decades of life, the fourth to the diagnosis of rheumatic carditis, the fifth part to therapy of rheumatic children. Although it is clearly evident that neither the efforts of the author nor those of other investigators have succeeded in adequately clarifying the fundamental questions concerning rheumatic fever, this orderly and comprehensive treatment of the findings at hand provides the necessary background for further studies on the subject.



TUBERCULOSIS AND GENIUS.

By Lewis J. Moorman. *University of Chicago Press, Chicago.* \$2.50. 9 x 5½; xxxv + 272 + 10 portraits; 1940.

The author apparently believes that some causal relationship exists between tuberculosis and the manifestations of genius, artistic genius particularly. However, in this book he does not seek to demonstrate this relationship but desires merely to reveal that tuberculosis is no obstacle to creative work. Therefore, he has compiled short biographies of 10 famous persons who probably had active clinical tuberculosis, or so the author believes. The biographies concern Robert Louis Stevenson, Schiller, Marine Bashkirtseff,

Katherine Mansfield, Voltaire, Molière, Francis Thompson, Shelley, Keats, and Francis of Assisi. In the elaboration of these biographical sketches the author has given free rein both to his imagination and to his knowledge of the course of tuberculosis. It would seem as if on the framework of the subject's life history the author has superimposed a typical tuberculosis case history, the same for all. An attempt is made to demonstrate that the infection was acquired in childhood from familial sources and that periods of exacerbation of the disease accompanied periods of great intellectual efforts. The style of writing resembles that of the Victorian romanticists so that, all in all, this book is definitely not recommended as a gift for sick friends.



PROGRESS IN MEDICINE. *A Critical Review of the Last Hundred Years.*

By Iago Galdston. *With a foreword by Henry E. Sigerist. Alfred A. Knopf, New York and London.* \$3.00. 8½ x 5½; ix + 347 + xiv; 1940.

This is not just another "romance" of the history of medicine revolved around the lives of a few trail-blazers. Rather it is a history of the ideas and philosophy underlying the great discoveries of bacteriology (the advance of the microbe theory of disease, and its fruits, the use of antiseptics, vaccines and serum, and modern sanitation), endocrinology, nutrition and the vitamins, and psychiatry which have been developed in the past century. Side-lights on the lives of the personalities in these fields (Pasteur, Koch, Erlich, Claude Bernard, Mesmer, Brown-Séquard, Braid, Charcot and Freud among a host of others), and the stories of how they came to think of this or observe that, add interest. Galdston writes with clarity and dignity and there is not a dull line in the book.



PREVENTIVE MEDICINE. *Sixth Edition, Revised.*

By Mark F. Boyd. *W. B. Saunders Co.,*

Philadelphia and London. \$5.00. 9½ x 6; xi + 588; 1940.

Boyd's book represents an endeavor to present briefly the salient features of modern preventive medicine. The material is presented in eight sections as follows: Diseases due to invading micro-organisms, Deficiency diseases, Occupational diseases, The puerperal state, Heredity and disease, Special aspects of hygiene and sanitation, Demography, and Public health. Since the last edition (cf. Q.R.B., Vol. 12, p. 125), rapid advances in knowledge of preventive medicine have taken place. In this new edition, revision in the chapters treating of sewage disposal, water supply, and deficiency diseases is particularly noteworthy. Much new material has been added to the sections dealing with syphilis, meningitis, pneumonia, tuberculosis, and yellow fever. An extensive bibliography is placed in the appendix and the book is completely indexed.



DISEASES OF WORKERS. *The Latin text of 1713 Revised, with translation and notes. De Morbis Artificum.* Bernardini Ramazzini *Diatriba.*

By Wilmer C. Wright. University of Chicago Press, Chicago. \$5.00. 9½ x 6; xvii + 549; 1940.

This is the seventh and one of the most interesting of the series of classical medical works republished under the auspices of the Library of the New York Academy of Medicine. Ramazzini's *opus*, aside from its historical value as the first systematic treatise on industrial hygiene, reflects the status of the medical art and science of his period. In addition, a first hand description is obtained of the working conditions and techniques of the 17th and 18th centuries. The translation is very readable and remarkably accurate. Included is a short biography of Ramazzini and the bibliographic references pertaining to him.



A TEXTBOOK OF PHYSIOLOGY. *Fourteenth Edition, Thoroughly Revised.*

By William H. Howell. W. B. Saunders Co., Philadelphia and London. \$7.50. 9½ x 6; xix + 1117; 1940.

Few texts with as long and distinguished a career as this one has had—it is now in its 35th year and 14th edition—have had the good fortune to be revised by the original author. The book has lived through a period of rapid development and great attainment in physiological research, and in preparing the present edition Howell says that it has been necessary to supplement "his own reading of original sources by frequent references to the many excellent reviews and summaries published by specialists in their several fields." In every way the volume maintains the high standard of previous issues.



OBSERVATIONS MADE DURING THE EPIDEMIC OF MEASLES ON THE FAROE ISLANDS IN THE YEAR 1846.

By Peter Ludwig Panum. Translated from the Danish by Ada Sommerville Hatchber. With a Biographical Memoir by Julius J. Petersen. Translated from the Danish by Joseph Dimont. And an Introduction by James Angus Doull. American Public Health Association, New York. 8 x 5½; xxxvii + 111; 1940.

This well-annotated translation of Panum's report is fittingly dedicated to the late Wade Hampton Frost. In his courses on epidemiology at the Johns Hopkins School of Hygiene and Public Health, Frost would always review this paper as an example of careful and systematic ordering and interpretation of facts. Because of these qualities the book certainly deserves to be brought to the attention of students of medical sciences. Included in appendices are also the reports of Dimont and of Manicus, respectively, on the same epidemic.



THE VIRUS: Life's Enemy.

By Kenneth M. Smith. The Macmillan Co., New York; The University Press, Cambridge. \$2.00. 7½ x 5; viii + 176 + 10 plates; 1940.

This volume in the *Cambridge Library of Modern Science* makes available to the general reader information of the greatest practical value which reads like a first-rate adventure tale. The history of virus study, the nature of viruses, and their mode of action are discussed in simple language. The author's treatment of the subject is authoritative, yet it is as concise and as interesting as a reporter's column, and as timely as newspaper accounts of the recent west-coast influenza epidemic.



RECENT ADVANCES IN SEX AND REPRODUCTIVE PHYSIOLOGY. *Second Edition.*

By J. M. Robson. With an Introduction by F. A. E. Crew. The Blakiston Co., Philadelphia. \$5.00. 8 x 5½; xiii + 329; 1940.

As in the first edition (cf. Q.R.B., Vol. 9, p. 489) the emphasis is placed on the hormones. In the past six years the progress in this field has been so vast that considerable changes and additions have been necessary. This edition is 80 pages longer than the first. New chapters include consideration of the properties of the male hormone and other androgens, the chemistry of the gonadic hormones, and the methods used in the standardization of the sex hormones. A selected bibliography has been added to each chapter, with those items which contain a detailed review marked with an asterisk. The volume is illustrated, and a subject index has been provided.



THE EMPEROR'S ITCH. *The Legend Concerning Napoleon's Affliction with Scabies.*

By Reuben Friedman. Froben Press, New York. \$1.50. 9½ x 6; 82 + [8]; 1940. Everyone who is familiar with the "Napoleonic pose" has his own theory, serious or otherwise, as to why the French emperor so frequently had his hand inside his shirt-front. In this little book an authority on some of the reasons why men—and women too—itch, gives his conclusions on the Little Corporal's physical

troubles. His evidence, though necessarily circumstantial, is good, and the diagnosis (dermatitis herpetiformis) he makes fits the picture historians have drawn of the dynamic, almost neurotic, conqueror.



BIOCHEMISTRY

TEXTBOOK OF BIOCHEMISTRY. *Second Edition, Revised.*

By Benjamin Harrow. W. B. Saunders Co., Philadelphia and London. \$3.75. 9½ x 6; ix + 439; 1940.

In this book the story of biochemistry is told in the form of closely-knit chapters. It covers the usual requirements of courses offered to medical, dental, agricultural, and general college students. Among the new material incorporated in the present edition is: Stanley's work on mosaic-diseased tobacco plants, Northrop's purification of bacteriophage, the multiple nature of vitamin A, the story of vitamin K and blood coagulation, sulfanilamide and sulfapyridine, the use of the nitrogen isotope in the study of protein metabolism, Kögl's work on d-glutamic acid and tumor tissue, newer conceptions of coenzymes and carriers in biological oxidation, and the chemistry of pantothenic acid, vitamin B₆, and vitamin E. The extensive references are placed at the end of each chapter. The emphasis has been placed upon reviews rather than on the original papers, though the latter are by no means excluded. Preference has been given to articles in English. An appendix giving in tabular form the nutritive value of foods, and a complete index conclude this excellent volume.



THE CHEMISTRY AND TOXICOLOGY OF INSECTICIDES.

By Harold H. Shepard. Burgess Publishing Co., Minneapolis. \$4.00. 10½ x 8½; iii + 383; 1940.

It is the avowed purpose of the author to present in this book the important facts and theories relative to insecticides,

including not only the chemical, physical and toxicological aspects, but also information regarding the history and commerce pertaining to this field. This text furnishes an excellent guide to the insecticide literature. Methods of insect control are not given except as the action of specific insecticides is illustrated. In addition to chapters on the history of insecticides, principles of insecticide toxicology, and quantitative toxicology of insecticides, stomach poisons, contact insecticides, plant derivatives and related compounds, insect fumigants, and miscellaneous chemical control are discussed in order. The volume is intended not only for college students, but for the many persons in public and private entomological pursuits who need a reference book on this subject. Extensive lists of references are given throughout the book and a good index is provided.



PROXIMATE COMPOSITION OF AMERICAN FOOD MATERIALS. U. S. Department of Agriculture. Circular No. 549.

By Charlotte Chatfield and Georgian Adams. Government Printing Office, Washington.

15 cents. 9 $\frac{1}{2}$ x 5 $\frac{1}{2}$; 91; 1940 (paper).

The formulation of a diet program requires a reasonably accurate knowledge of the composition of the various articles of food. This publication of the U. S. Department of Agriculture supplies information that is desirable, and presents in concise form an analysis of a large number of foods in general use in the United States of America. One table classifies fruits and vegetables according to the percentage of carbohydrates they contain. A second table includes an analysis of meats, fish, fruits, vegetables, cereals, cereal products, and miscellaneous products, showing the percentage of refuse, water, protein, fat, ash, carbohydrates, and acid they contain, and their fuel value (calories per 100 grams and per pound). There are also citations of literature containing more detailed and technical information as to variability in composition of various food products. Dietitians will find this publication useful.

VITAMIN E. *A Symposium held under the Auspices of The Food Group (Nutrition Panel) of the Society of Chemical Industry on Saturday, 22nd April, 1939 at the School of Hygiene and Tropical Medicine, Keppel Street, London, W.C. 1, England.*

Edited by A. L. Bacharach and J. C. Drummond. Chemical Publishing Co., New York. \$2.00. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; viii + 88; 1940.

As a spur to the pursuit of further knowledge, a symposium on vitamin E was held, April 22, 1939, at the School of Hygiene and Tropical Medicine in London, under the auspices of the Society of Chemical Industry. Fifteen papers and the discussions which followed their presentation are published in this monograph, which represents the proceedings of the conference. The meeting was a collaboration between workers in pure and in applied science, as the joint editorship of this volume by A. L. Bacharach of the Glaxo Laboratories, and J. C. Drummond of University College attests.



INVESTIGATIONS ON THE PHYSICAL AND CHEMICAL PROPERTIES OF BEESWAX. United States Department of Agriculture: Technical Bulletin No. 716.

By Charles S. Bisson, George H. Vansell, and Walter B. Dye. United States Department of Agriculture, Washington, D. C. 5 cents. 9 $\frac{1}{2}$ x 5 $\frac{1}{2}$; 24; 1940 (paper).

This thorough investigation of the properties of crude beeswax indicates that the properties of the impurities within the wax and not those of the wax itself, must be used for purposes of classification. The analysis of some 60 samples of crude wax included the determination of the melting point, the solidifying point, the density at 20° C., the refractive index at 80° C., the ash content, the saponification number, the acid number, the ester number, the ester-acid ratio, and the iodine number. Experiments dealing with the effect of metals on the color of waxes indicate that from the standpoint of cost and practicability, aluminum equipment is the most desirable for handling waxes. The value of sunlight in bleaching waxes is worthy of commercial application.

The text is well supplied with tables

and graphs, and is well documented in support of these significant findings.



SEX

SEX IN DEVELOPMENT. *A study of the growth and development of the emotional and sexual aspects of personality together with physiological, anatomical, and medical information on a group of 153 normal women and 142 female psychiatric patients.*

By Carney Landis and Coauthors. Foreword by Nolan D. C. Lewis. Paul B. Hoeber, Medical Book Department of Harper and Bros., New York and London. \$3.75. 9½ x 6; xx + 329; 1940.

Psychological investigations made by the questionnaire method on 154 "normal" and 142 psychotic or neurotic women form the basis of this analysis of the growth and development of emotional and sexual patterns in an attempt at an evaluation of the importance of psychosexuality in psychopathology. Anatomical, physiological, and medical findings for these same women were correlated with the psychological. Interpretive discussions accompany the case histories used to illustrate the normal sexually developed woman, the psychosexually immature woman, the homoerotic woman, the unhappily married woman and the psychiatric patient. A very wide range of variation in experience, emotion, and growth was apparent when an attempt was made for the construction of a composite biography of the course of normal psychosexual development. Few anatomical or physiological differences were noted between the normal group and the mentally disordered women, and therefore the definitely inferior sex adjustment in marriage in the latter group is assumed to be related "to certain unspecified psychological factors associated with the mental disease itself."

Although criticism may be made that many important aspects of the problem were not, and could not be, considered, due to the interview technique used, this is a definite contribution to the subject and an impetus for further research.

The volume concludes with four appendices containing the information forms used in the study, vital statistics, evaluation scales, and interscale relationships, respectively, a bibliography, an index of authors, and one of subjects.



REPORT ON THE SEX QUESTION.

By The Swedish Population Commission. Translated and Edited by Virginia C. Hamilton. Published for National Committee on Maternal Health, Inc. by The Williams & Wilkins Company, Baltimore. \$2.00. 8 x 5½; xx + 182; 1940.

This frank and calm scientific study of the sex question in Sweden may well serve as a model for similar studies in other countries that are following Sweden's lead in a decline in the birth rate. It is an abridged translation of the original report, and appendices which dealt with "special investigations of certain aspects of the material" have been omitted. Nevertheless it is well worth study by all students of population problems. In Sweden the declining birth rate has become a serious problem and has proceeded farther than in most other countries. The Commission emphasizes that the direct cause "must be sought in the sex life of the individual." To this end the main part of the report is devoted to the question of the extent of contraceptive practice and its evaluation from practical viewpoints—eugenic, medical and hygienic, psychological, economic, and demographic. Extramarital sex relationships, the extent of venereal diseases and the campaign against them, and prostitution are also considered. The report definitely demonstrates that the increase in the intentional practice of birth control (this term includes preventive birth control and induced abortion) "is the main, if not the only, responsible factor." Proposals for reorganizing sex instruction in the schools, and recommendations, which do not reek of propaganda, for a population program are made.

A SHORT HISTORY OF SEX-WORSHIP.

By H. Cutner. Watts and Co., London.

8s. 6d. net. $8\frac{1}{2} \times 5\frac{1}{2}$; xiii + 222; 1940. According to the author religions in their origins were closely connected with the mysteries of reproduction and fertility in man and nature, either alone or in combination with sun-worship. Probably the sex element in religion reached its height (or degradation) in the phallic cults which were curious though dominating elements in many ancient religions. These rites are still practiced today in one form or another among primitive peoples in various parts of the world, and in India. Cutner claims also that some of the Christian rites and symbols may be traced to a phallic origin—for example the fish, one of the favorite symbols of Christ was also a symbol of Venus—and in the freak sects that have sprung up from time to time in Europe and the United States the penchant for sex or its repression plays a prominent part. In this book the author provides the reader with historical information which is not easily accessible to the general public, for obvious reasons. The bibliography is confined to a few titles of books and there is an index.



BIOMETRY

A DETAILED PROOF OF THE CHI-SQUARE TEST OF GOODNESS OF FIT.

By E. Russell Greenwood, Jr. Harvard University Press, Cambridge. \$1.25. $6\frac{1}{2} \times 4\frac{1}{2}$; xii + [2] + 61; 1940.

The author states that, "the aim of this paper is to try to present a clear proof that will bridge the gap between what is known as the chi-square test of goodness of fit and the actual mathematical curve, the chi-square curve." He admits to the feeling, as many students in elementary statistics have, that something was being put over on him in regard to proof of the aforementioned test. The answer was not to be found in R. A. Fisher's *Statistical Methods for Research Workers*. Here he found only precise statements upon how to apply the test. The paper by Pearson, who originated the test, was found to be

little short of occult. It was only on reading T. C. Fry's article in the *Journal of the American Statistical Association*, Sept., 1938, that a crack of light appeared in the stygian void. With Fry's paper as a lever the world of chi-square was moved by the writer and the chi-square equation derived.

The lively, informal style of the work is very unusual in a statistical treatise and for this reason very pleasing. The interpretation to be placed upon "P" is discussed. A good bibliography is appended.



STATISTICAL PROCEDURES AND THEIR MATHEMATICAL BASES.

By Charles C. Peters and Walter R. Van Voorhis. McGraw-Hill Book Co., New York and London. \$4.50. 9×6 ; xiii + 516; 1940.

Many persons using statistical analyses in their work have often felt the need of a knowledge of the development of the formulas used. This volume was written to bridge the chasm between elementary courses, in which the formulas are given from a purely authoritative viewpoint, and the original papers, which are often highly mathematical in nature. The writers have produced a useful book.

The opening chapter deals with some of the elements of calculus. The following divisions treat of: measurement of central tendencies, variability, rectilinear correlation, the reliability of statistics, partial and multiple correlation, the normal curve, the chi-square test, curve fitting, and the technique of controlled experimentation.

Every chapter has appended a number of exercises and reference for further study. Several statistical tables are present at the end of the book and there is an index.



THE BULLETIN OF MATHEMATICAL BIOPHYSICS. Volume 3, Number 1, March, 1941.

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following

papers: Some remarks on the movement of chromosomes during cell division, by N. Rashevsky; On reinforcement and interference between stimuli, by G. Young; Studies in the mathematical biophysics of discrimination and conditioning I, by H. D. Landahl; Cellular forms and movements, by A. S. Householder.



PSYCHOLOGY AND BEHAVIOR

DYNAMICS IN PSYCHOLOGY.

By Wolfgang Köhler. *Liveright Publishing Corp., New York.* \$2.50. 8½ x 5½; [6] + 158; 1940.

The nineteenth century psychologists generally considered the field of their investigations as discontinuously separated from the rest of nature. This attitude tended to give them more intimate contacts with the quack element among the phrenologists than with the legitimate biological sciences. In the twentieth century a normal reaction set in, and the value of the biological sciences as the only possible foundation on which a truly scientific psychology might be erected began to be appreciated.

Köhler swings the pendulum vigorously to the other extreme. Not unmindful of the importance of biology, he goes beyond it to the physics of Faraday and Clerk-Maxwell for fundamental principles. The result is that his book suffers from the attempt to crowd too much material into too small a space, to pack too many thoughts into too few words. For instance, many times the author describes experiments and from the observed results draws conclusions which sometimes seem irrelevant or even contradictory. These unsatisfactory deductions might have been clarified had the author set out a few more of the links in his chain of ratiocination.

Probably most readers will find the most stimulating part of the book to be the discussion in the final chapter of the place of theory in science. Today the emphasis in much scientific research seems to be placed chiefly on the accumulation of facts, rather than on their classification and interpretation. Perhaps this is due

to the fear of humiliation that an author must feel when a theory which he has formulated is forced to give ground to a subsequently verified fact that stubbornly stands in its way. Köhler evidently believes that a scholar manifests his character best not by the tenacity with which he maintains a theory but by the readiness with which he accepts modification to it to bring it into agreement with changing conditions. He ably argues the case for scientific theory and points out that the greater scientists are characterized by a sense of humility and reverence such that he is not discouraged by the thought that his creative achievements (and theory is the only creative achievement of science) must of necessity undergo modification as the result of the discovery of new facts.

The author has assumed the rôles of Aaron and Hur to the theoretic biologist's Moses, for which the theoretic biologist has every reason for gratitude.



CONDITIONING AND LEARNING.

By Ernest R. Hilgard and Donald G. Marquis. *D. Appleton-Century Company, New York and London.* \$2.75. 8 x 5½; xi + 429; 1940.

This highly technical survey of the investigations of Pavloff and his satellites covers the entire field of experimental psychology in a thoroughly commendable manner. From it we learn that Pavloff never considered himself a psychologist; he was a specialist in neurology. But the influence of the experimental technique which he developed defies mensuration, for it is difficult to imagine how the researches of such outstanding figures in experimental psychology as Bekhterev, Watson, or Yerkes could have been initiated without Pavloff to point the way. The procedure by which rats are taught to emulate Ariadne, or chimpanzees to pile Ossa on Pelion, while not exactly homologous to that by which dogs can be made to salivate, is somewhat similar, and the reactions may be conditioned in somewhat the same way. All this receives detailed treatment in this comprehensive compendium.

The authors state that in 1915 Watson lectured on respiration and heart rate. Unfortunately they do not discuss these instances of conditioning, for the effect that such might have on philosophic thought is quite considerable.

The work here under discussion has a subject index of ten and one-half pages, and a bibliographic index of 973 separate items, but its most helpful feature is a twelve-page glossary—not an ordinary glossary, but one that contributes vitally to the reader's comprehension of the book.



THE TREE OF LIFE of the Human Personality.

By Mary Macaulay. C. W. Daniel Company, London. 2s. 8½ x 5½; 29 + 2 folding plates; 1940 (paper).

The frontispiece of this pamphlet is a design of a tree representing the positive aspects of the psychological development of man from babyhood, through childhood and adolescence, to full maturity; at the back is one showing the negative aspects. These are so placed that they may be turned out for consultation while reading the interpretations which form the subject matter. Among the conclusions we find:

It may be said . . . that the endless conflicts centering round the question of personal liberty come mainly from *abuses in the nursery*. The incoming personality of little children is seldom treated with due respect, or its innate dignity scrupulously maintained. A common cause of early loss of self-respect and self-confidence is a cruelly restrictive material environment, in other words, dire poverty. Parental attitudes of possessiveness, and these, too, are general in all countries, violate personal liberty from the moment of birth (if not before). Parental and social ignorance of, and indifference toward, children's psychological needs. . . . These conditions produce unbalanced people, tyrants, snobs, bullies and aggressors and the multitude of their too docile unheroic victims or followers.

The above quotation serves also to illustrate the style of writing.



EFFECTS OF QUANTITATIVE VARIATION OF FOOD-INCENTIVE ON THE PERFORMANCE OF PHYSICAL WORK BY CHIMPANZEES. *Comparative Psychology Monographs, Volume 16, Number 3, Serial Number 82.*

By Frank M. Fletcher. *The Johns Hopkins Press, Baltimore.* 75 cents. 10 x 6½; 46; 1940 (paper).

This investigation was undertaken to determine the quantitative relationship between size of incentive and the work the chimpanzee would do to obtain it. Among the results obtained were:

All measured characteristics of pulling-in behavior were significantly affected by the size of the incentive. . . . With a certain constant resistance (which varied from subject to subject), frequency of response increased from 0 per cent to 100 per cent with increase in size of the incentive. . . . The results indicate that in a work situation a chimpanzee tends to develop a fairly constant method of pulling with a given kind and amount of resistance, and if a food-incentive is drawn in at all, it is pulled in this way.

Large individual differences were found to exist among the four animals used. Various factors, such as number and size of other incentives presented in close temporal proximity, training, satiation, fatigue, food-hunger, etc. affected the relationship of size of incentive and resistance level to frequency of response. A short bibliography is appended.



**DE OMNIBUS REBUS
ET QUIBUSDEM ALIIS**

THE SOCIAL MIND: Foundations of Social Philosophy.

By John Elof Boodin. *The Macmillan Co., New York.* \$3.50. 8 x 5½; xi + 593; 1940.

Boodin's book, the product of a life-time of study and thought, is far too complex to be adequately dealt with in a brief review. It is a book for the student and the intelligent lay reader, if he is willing to devote the time necessary to grasp its import. The thoughtful reader, once well within its pages, will find it absorbingly interesting.

Basic in the author's writings since early in the present century are the two concepts, creative synthesis (epigenesis, emergence), and wholism or gestaltism. For the benefit of those who have not been following modern philosophical

thought we give Boodin's clear but concise definitions of these terms:

Creative synthesis (epigenesis, emergence) means that new characters, not present in the constituent factors or conditions, appear as a result of the interaction. Wholism means that individuals or events can be understood only as figuring in a whole or gestalt. It is important to bear in mind that this whole must have reference to time as well as to space. Social relations illustrate both emergence and wholism. The two concepts, however, do not always go together. Casual social relations may influence human beings, but they do not constitute a whole or group.

Psychology in the past has started with the idea of isolated minds and from this postulate an attempt has been made to comprehend how one mind can understand and evaluate another by means of analogical inference. The author believes that "we must start with the postulate of intersubjective continuity [the immediate consciousness of mental responsiveness] as an elementary fact." Mind, like matter, must be conceived as existing in fields with their own continuities and their own play of parts.

It is pointed out that social minds must be real if they possess characteristics analogous to those of particular minds. One of these important characteristics to which the author gives much attention is *fusion*. In social fusions, the quality of the components makes a difference. The French fusion is different from the Anglo-Saxon fusion; the feminine fusion differs from the masculine fusion. Social minds are far more numerous than personal minds since "social continuities intersect individual centers in an indefinite number of planes."

A careful reading of the section on "The existence of the social mind" will well repay the reader, for it lays the basis for a clear understanding of the latter part of the book in which the author discusses social systems, the organization of cognition and of will, the crisis of our present civilization, education and progress, and finally, social immortality. He shows the way in which the desires and thoughts of humanity are woven into social patterns and what direction must be taken in the future if we are to meet the demands for a real democracy.

DIALECTICS OF NATURE.

By Frederick Engels. Translated and Edited by Clemens Dutt with a Preface and Notes by J. B. S. Haldane. International Publishers, New York. \$3.00. 8½ x 5½; xvi + 383; 1940.

Frederick Engels was a much misunderstood genius. His unfortunate partnership with Marx, under which the former did most of the work and the latter got all the credit, has kept Engels pretty much in the background, so much so that the present work is only now being published in English translation for the first time, more than half a century after it was written.

Engels' object seems to have been to cover the entire field of science. Nothing was too small or insignificant to be worthy of his attention; even psychic phenomena, the authenticity of which he rejected *in toto*, has been given one chapter. As we look back over the progress of science during the past sixty years this treatise seems strangely prophetic. Engels believed that the solar system condensed from a spiral nebula, the planets all having consequently the same temporal age, a belief commonly held today, but which has nothing in common with the nebular hypothesis of Laplace and Kant. The latter believed that the planets were formed in succession by the condensation of rings thrown off from the solar equator by tangential force. Engels propounded his theory at a time when the entire field of astrophysical thought was dominated by Laplace.

In the same way his views on biological theory were far in advance of his time. In the preface of this edition, contributed by J. B. S. Haldane, that writer regrets that he was not earlier acquainted with Engels' comments on Darwin, as they would have spared him much muddled thinking.

Unfortunately Engels, like Franklin, was too early diverted from the pursuit of natural to that of political science, and modern civilization is the poorer from this. Had Engels completed his task of self education in the natural sciences his political conclusions would have had a more solid foundation and would have been correspondingly more

significant and influential. As it is he was a most profound thinker, but his manuscript was left in an extremely sketchy form, is quite ungrammatical, and composed largely of disconnected notes, so that a great deal of editing has been necessary. As a historic document it is full of interest, but as a contribution to modern scientific thought it has not been very successful.

There is a bibliography and an index, but neither seems to be proportionate to a work of this size.



LIFE ON OTHER WORLDS.

By H. Spencer Jones. *The Macmillan Co.*, New York. \$3.00. 8 x 5½; x + 299 + 17 plates; 1940.

Does life exist elsewhere than on earth? Today man is better prepared than ever before to answer this question of the ages. Jones has impressively revealed how astronomy, biology, physics, and chemistry have all contributed to the rapid advance in knowledge of our own and other stellar systems. Living things are aggregates of large chain molecules in a colloidal state. Prerequisite for life are the materials and conditions from which such molecules can be formed. A further necessary, but by no means sufficient, condition is the existence of elements and compounds in a physical and chemical state which the organism requires for its metabolic processes. In addition there must be no lethal temperatures, pressures, or chemical compounds. The conditions which exist on a certain world can be estimated from its size and distance from the parent sun, and can generally be confirmed by use of a spectroscope and delicate thermocouple.

One by one Jones eliminates the other planets of our solar system, with the possible exception of Mars where there is strong evidence of vegetation. Indeed, there may at one time have been animal life on Mars. If life does exist elsewhere it need be similar to ours only in its fundamental properties, but modified in form in accordance with the conditions of the other world. The limited bounds within which life is possible would lead

us to believe that ours is the only such existence. On the other hand it is difficult to believe that there may not somewhere among the thousands of millions of stars be planetary systems wherein the precise conditions are fulfilled.



SILVER IN INDUSTRY.

Edited by Lawrence Addicks. Reinhold Publishing Corp., New York. \$10.00. 9 x 6; vii + 636; 1940.

Among the many subjects covered in this volume biologists will find two of especial interest. The first treats with the oligodynamic effects of silver. The second treats with the fungicidal properties of silver. Carl Nägeli in 1893 showed that pure water brought into contact with clean metallic surfaces was lethal to *spirogyra*. Subsequent analysis showed the concentration of the metal to be of the order of 10^{-8} . The aforementioned effect seems to be due to the presence of metal ions dissolved in the water. Oligodynamic water is not permanent and the lethal property slowly disappears if the source of ions is removed. It has also been found that if the metal concentration is not sufficient for killing, a stimulation occurs. Differences in media, pH, temperature, cell concentration, etc., may account for many of the discrepancies found in the literature. However, it seems that the physiological behavior of the cells must also play an important part. This appears to be particularly true in view of the finding that proteolytic bacteria are generally more resistant than the saccharolytic types.

The volume is well illustrated and indexed. Each chapter has an extensive bibliography appended at the end of the book.



SCIENCE AND THE CLASSICS.

By D'Arcy W. Thompson. Oxford University Press, New York and London. \$1.00. 6½ x 4½; viii + 264; 1940.

To those who know Thompson only by his contributions to the mathematics of

metabolism this work will come as a delightful surprise, for it reveals a mind of such broad culture that it is equally at home in the fields of astronomy, literature, biography, and the foreign languages. It is a collection of brief essays, each complete in itself, originally delivered as lectures not only at St. Andrew's University, but at others in England and France as well.

The essay on Aristotle is extremely timely, in view of the fact that in another work (also reviewed in this issue) a younger author has seen fit to attempt to deflate this ancient authority in somewhat derogatory tone. The reader who seeks an unprejudiced narration of what Aristotle really accomplished in the way of natural science, and how he surpassed many of his successors, and why he dominated philosophical thought for about twenty centuries will find this all lucidly expounded in this work, which is characterized by its genial humor as well as by its erudition. The discussion of the "Golden Section" is quite striking.

To those who have become stale as the result of too close concentration on specific problems close at hand this book is highly recommended.



THE STORY OF SUPERFINISH.

By Arthur M. Swigert, Jr. Lynn Publishing Co., Detroit. \$5.00. 9 x 6; [12] + 672; 1940.

Man has long recognized the truth inherent in the statement that a chain is no stronger than its weakest link. The writer of this book paraphrases the foregoing when he states that a machine is only as efficient as its least satisfactory load-carrying bearing surface. The realization of this has focused the attention of scientists and engineers upon the relationship existing between the boundary layers of metallic surfaces.

The subject is developed from the historical point of view. Correlatives dealing with machine methods and techniques used in testing the surface finishes of materials are given. Among the methods used to test finished surfaces are electronic diffraction, magnaflux, and

methods of amplifying the sound of a stylus drawn over the surface.

The many tables and illustrations clarify and amplify the text. No bibliography has been provided and the brief index is quite inadequate.



LOOK AT LIFE! *A Collection of the Nature Photographs.*

By Lynwood M. Chace. Alfred A. Knopf, New York and London. \$3.50. 10 x 7; 250; 1940.

Every now and then someone comes along and shows us what we are missing, and this Chace has done with the lens of his camera. This book is a unique collection of nature photographs, but what characterizes these pictures is not mere scientific exactitude, for their maker does not hesitate to pose his subjects sometimes, the better to display them. Much ingenuity has gone into some of his achievements. In certain of the more remarkable photographs in this collection the accuracy of the lens transcends imagination. It becomes the eye of a veritable magician, perceiving that which is hidden from unaided human vision. And Chace has an instinct for significant design. Nothing is too ugly or affrighting, by commonplace standards, for him to look deeper at it, and find its significance and perhaps a revelation of its genuine aesthetic value. Indeed this is a most interesting and absorbing volume.



FRENCH-ENGLISH SCIENCE DICTIONARY for Students in Agricultural, Biological, and Physical Sciences.

By Louis De Vries with the Collaboration of Members of the Graduate Faculty. McGraw-Hill Book Co., New York and London. \$3.50. 7 x 5; viii + 546; 1940.

Like its companion volume, the *German-English Science Dictionary* by the same author, this compact dictionary of 43,000 entries will prove an invaluable aid to graduate students and workers in the sciences. Terms are included covering

entomology, embryology, cytology, physiology, morphology, genetics, ecology, chemistry, physics, botany and medicine and a general vocabulary. Naturally not all names of animals, insects, plants and chemicals could be included. Many forms of irregular verbs are given with at least one meaning, and for these the infinitive form is marked in parentheses so that the student may consult this verb part for further meanings. This feature will be appreciated by persons with a limited knowledge of French grammar.



VEGETABLE VARIETY: or How to Enjoy a Meatless Meal.

By Ann Gurney. Illustrated by Katherine Ogilvy. The Medici Society, London. 1s. 6d. 9 x 5½; 37; 1940 (paper).

This little book with something over 100 recipes for the cooking of vegetables turns out to be something quite different from what one ordinarily expects an English cook book to be. While one occasionally comes across recipes that

call to mind the traditionally poorly cooked English vegetables, a large number of them seem to be well worth trying. Many suggestions are given that will give new life to old dishes. An added interest is given the book by illustrations of old prints and line drawings by Katherine Ogilvy.



OUTDOOR PORTRAITURE. Problems of Face and Figure in Natural Environment.

By William Mortensen. Camera Craft Publishing Company, San Francisco. \$2.75. 9½ x 6½; 142; 1940.

By far the greatest number of photographs taken by amateurs are outdoor pictures of people. Hence there is need for an authoritative book dealing solely with this subject. Consideration is given first to the mechanism of proper equipment and handling of the camera, then to those bugbears of the amateur—lighting, background, and composition. Both positive and negative suggestions are well depicted by over 100 illustrations.



THE QUARTERLY REVIEW of BIOLOGY



OBSERVATIONS AND EXPERIMENTS ON MATING BEHAVIOR IN FEMALE MAMMALS

By WILLIAM C. YOUNG

Yale Laboratories of Primate Biology

INTRODUCTION

MOST investigators of cyclic reproductive activity in female mammals have been more interested in the functional basis of the morphological changes and less interested in an analysis of the factors underlying the parallel changes in behavior. This inequality of emphasis probably can be attributed to the circumstance that the most stimulating of the early studies were initiated by anatomists and to the belief held for many years that external manifestations of heat are not sufficiently well defined to lend themselves to study by quantitative methods. As things have turned out, this early neglect of the behavioral responses is not altogether unfortunate because it has since become apparent that little progress could have been made had it not been for the splendid endocrinological background established by the experimental anatomists and the biochemists they enlisted in their aid. Only after this background was established, did it become possible to induce heat almost at will and to look forward to an investiga-

tion of factors involved in the regulation of its character and to a comparative study.

Heat and estrus, as the words are used here, refer to the physiological state of the female when she will permit copulation, but this criterion of heat has not always been insisted on. In the first modern investigations of reproductive activities when external signs of heat were thought to be absent or slight, the detection of a sequence of vaginal changes which recur at cyclic intervals and about the time of heat was regarded as a reliable test of the estrous condition in the guinea pig, mouse, rat and opossum (Stockard and Papanicolaou, 17, 19; Allen, 22, 23; Long and Evans, 22; Hartman, 23a). Consequently, in subsequent experimental studies in which these species were used, a vaginal smear picture devoid of leucocytes and composed of nucleated epithelial cells and cornified cells, or cornified cells alone, was frequently assumed to be diagnostic of heat in the absence of a mating test.

More often than not, this assumption was undoubtedly correct, but subsequent observations have revealed that in any

investigation of mating behavior in which it is important to ascertain the beginning and end of heat or anything about its character, a more exact test is necessary. It has been shown, for example, that in several species the cyclic vaginal changes are of a type more or less distinct, but for one reason or another they are of doubtful value in the diagnosis of heat, viz., the dog (Evans and Cole, 31; Leathem and Morrell, 38, 39), the cat (Bard, 39), the sow (Wilson, 26), the cow (Hammond, 27; Cole, 30), the ewe (Grant, 34; Cole and Miller, 35; Höcker, 38), and the horse (Aitken, 27; Schtschjekin, 30), although Mirskaia (35) states that with rare exceptions cornified cells only were found during estrus in 45 mares.

In other species, even those in which the vaginal changes are most clearly defined, the condition normally associated with heat may be found in its absence, or heat may occur when its existence would not be suspected from the vaginal condition (Ishii, 22; Long and Evans, 22; Slonaker, 27; Smith and Engle, 27; Oslung, 28; Hemmingsen, 29, 33; Evans, Meyer and Simpson, 33; Witschi and Pfeiffer, 35; Ball, 36a, 37a; Young, Boling and Blandau, 41, for the rat; Smith and Engle, 27; Marrian and Parkes, 30; Voss, 30; Wiesner and Mirskaia, 30; Engle, 31; Lewis and Wright, 35; Snell, Fekete, Hummel and Law, 40, for the mouse; and Fellner, 32; Young, Dempsey and Myers, 35b; Young, 37, for the guinea pig).

A third reason for not relying on the vaginal test of heat in a study of mating behavior is that the vaginal changes normally associated with heat are not specific for heat. Evans and Bishop (22) and Evans (28) have shown that the constant cornification of the vaginal epithelium which results from vitamin A deficiency in the rat is not accompanied by a continuous state of heat, and Wade and Doisy (35)

and Emery and Schwabe (36) have shown that the method of obtaining material from the vagina may produce complete cornification without other symptoms of heat.

Because the presence of certain cell-types in the vagina does not always indicate a willingness to copulate, much of the literature in which there is no proof of heat beyond the demonstration of vaginal estrus is not discussed in the review which follows. This omission is not intended to reflect any lack of appreciation of the past or prospective value of the vaginal smear technique for investigations of reproductive activities. In their studies of reproductive behavior the reviewer and those associated with him frequently employ this test routinely, but they find it necessary to rely on supplementary tests in order to be certain that the animals are sexually receptive.

OBSERVATIONS ON THE CHARACTER OF MATING BEHAVIOR

Some information has been obtained about the mating behavior of representatives of all orders of mammals except the armadillos, manatees, and dolphins, whales and porpoises. Quite naturally we know most about species which are used in the laboratory, about those whose domestic value is such that a careful study of breeding habits has been encouraged, and about those which have been observed to breed in captivity in zoological gardens. Data which have been obtained from free-living forms are scanty at the best, but they are sufficient to indicate that an essential similarity exists between the main features of behavior observed under laboratory and natural conditions. They also give us glimpses here and there which contribute to the assembling of a comparative picture.

The albino rat

The non-pregnant albino rat comes into heat at intervals of four to five days throughout the year and usually after 6 p.m. When she is not willing to accept copulation, the female pays no attention to the male and if approached too closely may defend herself violently with one hind leg or even fight if the male is aggressive (Stone, 22; Wang, 23; Hemmingsen, 33). The beginning of heat is rather abrupt, and after an initial period of relatively intense responses, there is a more gradual return to a loss of sexual interest. The movements during this period are quick and darting, often in hops accompanied by a quivering of the ears or the entire body, and the female does not run away from the male, except that following a moment of smelling or licking by the male, she runs forward a short distance and halts where she is usually overtaken and caught in the copulatory clasp. When mounted by the male or fingered on the hindmost part of the back and around the base of the tail a lordosis or opisthotonus is shown which consists of an arching of the back brought about by depressing the lumbar and elevating the sacro-coccygeal region (Long and Evans, 22; Stone, 22; Wang, 23; Warner, 27; Hemmingsen, 33; Ball, 37a; Blandau, Boling and Young, 41). Hemmingsen regards this behavior as an invariable criterion of heat, but because of the observation by Long and Evans that a slight lordosis may be elicited at any time during the cycle by firmly inserting a speculum into the vagina, he questions that lordosis without the quivering of the ears and the darting movements is a sufficient proof of heat. It may be that females from which only a weak lordosis can be elicited, will not always mate, but Blandau, Boling and Young have found that when a strong lordosis is given the

female will mate regardless of the other responses.

In addition to the above described characteristics of the estrous period, there is an increased muscular or running activity (Wang, 23, 24; Slonaker, 24, 27). One of Slonaker's rats ran as much as 38 miles during a 24-hour period which is assumed to have included the period of heat. This running activity, like the epithelial changes in the vagina, may be displayed in the absence of heat (Hemmingsen, 33; Hemmingsen and Krarup, 37b), but usually the peak of activity coincides with the time of heat.

Many variations in the character of the responses and in the length of heat are shown from animal to animal and from cycle to cycle in the same animal, although in a group of animals observed over 7 and 8 consecutive heat periods a considerable consistency of behavior was shown (Blandau, Boling and Young, 41). Often a more intense response is given to an aggressive male (Stone, 22; Hemmingsen, 33; Ball, 37a). The differences that are shown do not limit the usefulness of behavioral signs in the identification of heat. On the contrary, they enabled Hemmingsen and Ball to establish carefully graded systems by means of which 12 intensities of estrous responses can be determined and compared. In Hemmingsen's system the two lowest stages represent merely a decrease in unwillingness to comply with the male. The next higher two represent the lowest degrees of heat; the female shows a slight lordosis, but does not permit copulation. Beyond these stages there is an increasing willingness to respond to the male until, in the highest intensities shown, the female actually takes the initiative in placing herself demonstratively before the male or displays sexual excitement in the presence of normal females. In the opin-

ion of the reviewer, a simplification of the systems devised by Hemmingsen and Ball would be desirable, but apart from this adjudged fault they represent a beginning toward the study of sexual behavior by quantitative methods which is wholly admirable.

The length of heat in the rat is given as 4 to 8 hours (Ishii, 22), 3 to 12 hours (Long and Evans, 22), and 3 to 21 hours (Ball, 372). The latter figures appear to be most nearly correct if we may judge from the average length of 13.7 hours, range 1 to 28 hours, determined by Blandau, Boling and Young (41).

The length and character of the estrous reactions may be affected by copulation although the point is by no means clear. Hemmingsen states that if a plug is allowed to form, the response of the female sometimes becomes antagonistic immediately afterward, but usually it will again show heat after a short while. Blandau, Boling and Young (41) found that the average length of heat was slightly but nevertheless significantly shorter in twelve animals which were allowed to mate at the beginning of heat. Neither set of observations, however, is completely convincing partly because allowance was not made for the possibility of a quantitative relationship between the amount of stimulation and the continuation of heat such as Ball (34a) found between the amount of stimulation and the production of pseudopregnancy.

A form of estrous behavior occasionally seen in albino rats is best referred to as male-like, mounting or homosexual behavior. When it is displayed the females act the part of the male by mounting other females and making all the movements of copulation except for rolling back and cleaning the genitalia afterwards (Long and Evans, 22; Hemmingsen, 33; Beach, 38b; Ball, 40). More recently, however,

Beach (41) has seen untreated females execute the complete masculine pattern. In his earlier publication Beach (38b) suggests that mounting is associated with intense heat reactions, but Hemmingsen observed mounting by a female in which only a low degree of heat was being shown. Beach also notes that this "abnormal behavior" was not observed in the sexually experienced female, but no evidence for or against the validity of this observation is given by Long and Evans or Hemmingsen. The frequency with which this behavior is displayed was increased by injecting normal females with testosterone propionate (Ball, 40). The pattern differed from that displayed by untreated rats only to the extent that the genitalia were cleaned afterwards.

In addition to its cyclic occurrence in the non-pregnant rat, estrus is displayed by most animals soon after parturition. Earlier observations by Tsai (25) and Slonaker (25) yielded data which are less definite than those recently reported by Blandau, Jordan and Soderwall (40). The latter authors found that postparturitional heat was displayed by 27 of 29 animals, its length averaged 10 hours, which is somewhat less than that of heat periods in non-parturient females, and the length of the interval between the end of parturition and the beginning of heat averaged 18.5 hours, range 4 to 37 hours.

Occasionally estrus is displayed during pregnancy (Long and Evans, 22; Nelson, 29) and lactation (Slonaker, 25), but under such circumstances nothing is known about its character. It is merely reported that heat was displayed by one animal on the 4th and 14th days of pregnancy, by another on the 16th day, and by a third (Nelson's) on the 5th, 13th and 17th days of pregnancy. Slonaker states that mating tests made at some of the peaks of activity during lactation showed that the peaks

represented heat. The reviewer has found no reference to the occurrence of heat during pseudopregnancy.

Despite the extent to which the rat has been used in studies of reproductive activities, the relationship of the time of ovulation to heat has long been uncertain. Long and Evans concluded that in most animals ovulation occurs several hours after heat, but the results from a more recent investigation, in which the time of ovulation was related to the beginning of heat as determined by the willingness to copulate, have shown that in most animals ovulation occurs shortly before the end of heat. In a colony of animals in which the length of heat averaged 13.7 hours, no case was found in which ovulation had begun within six and one-half hours after the beginning of heat, but by the tenth hour it was complete in most animals (Boling, Blandau, Soderwall and Young, 41).

Heat without ovulation in normal appearing adult rats has only recently been described. In two animals in which ovulation had not occurred by the twelfth hour, microscopic examination of the ovaries disclosed that normal luteinization of the large follicles had not occurred and that ovulation would have been unlikely. In two other animals in which a longer interval elapsed between the beginning of heat and death, the evidence was even more convincing (Boling, Blandau, Soderwall and Young, 41).

Under experimental conditions, heat without ovulation has been reported in infantile rats. Mahnert (30) induced heat in 4-week old individuals by means of prolan injections. Ovulation was not induced, but corpora lutea-like bodies were present. The converse situation, namely, ovulation without heat in otherwise normal animals, has been described by Ishii (22), Hemmingsen (33) and Boling, Blandau, Rundlett and Young (41).

Wild rats

Descriptions of heat behavior have been found for three species of wild rats, the brown or Norway rat (Miller, 11), the Texas rice rat (*A. Svihla*, 31), and the wood rat (Wood, 35). They are rather sketchy but sufficiently complete to indicate that most of the elements of estrous behavior seen in the white rat are present in these wild species.

At least one, the brown rat, normally comes into heat after 5 p.m. The rice rat, if in heat, will go through characteristic mating reactions. If not, she will have nothing to do with the male and will fight him even to the point of killing him if he is too aggressive. The brown rat in full heat is also less pugnacious than at other times. When in heat both the wood rat and the rice rat take the initiative. After some preliminary sniffing, the female wood rat places herself directly in front of the male with her tail curved to one side. The female rice rat will follow the male about the cage, smelling of his genitalia until he turns and follows her. She then gives the appearance of starting to run away, but stops after taking a few steps and accepts copulation. The brown rat is more active when she is in heat than at other times.

The female brown rat is similar to the white rat in that the willingness to mate depends to some extent on the dominating ability of the male. Miller states that he never observed a female to mate with a male smaller than herself, but indicates that a pugnacious female, if placed with a larger male which could boss her, would mate without opposition.

Copulation does not appear to affect the length of heat in the wood rat or brown rat. A rice rat, on the other hand, is reported to have refused further attentions from the male after an initial period during

which several copulations took place, but it cannot be certain that this species was observed beyond what may have been an initial period of antagonism similar to that seen in the albino rat.

Postparturitional heat has been observed in the rice rat, the females of which mate within 10 hours after birth of the young (A. Svihla, 31). Heat may also occur in this species during lactation, for Svihla states that after several copulations, if she had a litter of young, the female went to her nest and nursed them.

The mouse

The estrous behavior of the mouse is less definite than that of the rat; at least no reliable method for detecting the time of heat has been found which does not require a mating test. Consequently, less is known about the mouse than the rat. As in the latter species heat occurs at intervals of 4 to 5 days and is predominantly nocturnal (Lewis and Wright, 35; Snell, Fekete, Hummel and Law, 40). Its average length and range of variation are not known. According to Snell, Fekete, Hummel and Law, an estrous period of less than 24 hours is indicated; its length is perhaps nearer twelve hours. Certain species of mice may have the distinction of attaining sexual maturity sooner than any other mammal. Bailey (24) states that the female meadow mouse mates when she is 25 days old, and Hatfield (35) observed copulation in three females when they were 21 and 22 days old.

In several respects the behavior of the mouse resembles that of the rat. When the female is being pursued by the male, often after she has led him on (Svihla, 30, 32; Hatfield, 35), she will run a short distance and stop, immediately after which mating takes place. When she is being served by the male she frequently bends back her head and, in doing so, tends to

display a lordosis. Non-estrous female meadow mice (Bailey, 24; Hatfield, 35), red-backed mice (Svihla, 30), and deer mice (Svihla, 32) are pugnacious toward the male and the reviewer's recollection is that the behavior of non-estrous white mice is not different.

The effect of copulation on heat is not clear. The red-backed mouse, deer mouse and meadow mouse are said to lose their desire to mate after a few copulations, although Bailey states that some meadow mice will accept attentions promiscuously. Hemmingsen observed 7 ridings in two hours in an albino mouse, but notes that the female squealed and sometimes ran away from the male. Decision is difficult, but some effect of copulation is suggested. As with the rice rat, however, the question arises if normal heat behavior may not be resumed after a short post-copulatory period of antagonism.

Heat within 12 hours postpartum is said to be the rule although heat was not found in two species of the deer mouse (Svihla, 32) and in the harvest mouse (R. D. Svihla, 31) immediately after birth of their litters. For species in which postparturitional heat is known to occur, nothing is known about its character.

Watt (31) describes a case of heat during pregnancy, but since the mouse was in a protracted labor, the reviewer is inclined to regard this as an instance of heat which ordinarily would have occurred postpartum. The best evidence for heat during pregnancy is that presented by Crew and Mirskaia (30) who report its occurrence in 6 of 100 pregnant females. In each of the 6 animals mating occurred only once and then (4th, 8th, 10th, 14th, 15th or 16th day) not always at a time when it would have been expected had the animals not been pregnant.

Data bearing on the time of ovulation with respect to heat have recently been

reported by Snell, Fekete, Hummel and Law. In the stock they used the interval between the onset of estrus and ovulation was quite variable, but as a rule probably did not exceed 2 or 3 hours. Since the length of heat may be about 12 hours, the implication is that ovulation occurs during the first half of heat. If this is true for all strains, the mouse differs in this respect from the rat.

The possibility that ovulation is not always accompanied by heat is suggested by Lewis and Wright (35). In their experiments eggs were recovered from ten animals which did not copulate and in which, presumably, heat did not occur. Their data also indicate that heat is sometimes shown in the absence of ovulation. Of 103 mice which copulated, no evidence of ovulation is reported in immature females following the implantation of anterior pituitaries (Engle, 31), and following the destruction of gametogenic tissue by x-ray treatment of the ovaries (Parkes, 26, 27a, 27b).

The guinea pig

The estrous responses of the guinea pig are definite and easily recognized (Rein, 83; Miss Lathrop in Loeb, 14; Draper, 20; Ishii, 20; Tresidder, 22; Avery, 25; Louttit, 27; Young, Dempsey and Myers, 35b; Young, Dempsey, Hagquist and Boling, 37, 39). Lordosis which consists of a straightening of the back and an elevation of the pelvis is an unmistakable sign of heat when it can be obtained repeatedly. Frequently it is accompanied by a guttural vocalization and by the pursuit and mounting of other females and even males, but both types of behavior may be displayed independently of heat and therefore neither is a specific diagnostic of heat. The estrous responses are displayed most vigorously at the beginning of heat. Thereafter, they subside gradually until the

end of heat when the animal again becomes repellent and by kicking vigorously with one hind leg or snapping with the mouth, fights away any advance by the male or any attempt to stroke her by the investigator. Differences exist in the intensity with which the estrous responses are given and in the length of time they can be elicited. Unfortunately, no method of evaluating the intensity of the responses has been worked out as Hemmingsen and Ball have done for the rat. Instead length of heat has been employed in measuring differences. It averages 8 to 9 hours, range 1 to 41.5 hours, although any heat longer than 20 hours is exceptional. From animal to animal a tendency exists for heat periods of a certain approximate length to be displayed (Young, Dempsey, Hagquist and Boling, 39).

In females in which heat tends to be long, it frequently is intermittent with intervals when the female will not mate inserted between periods of receptivity. This type of heat has been referred to as the "split estrus," a term which was perhaps not wisely chosen; "intermittent estrus" probably would be better.

As with the rat and mouse, the effect of copulation on heat is not clear. Tresidder seems to doubt that its course is affected by copulation, but Avery's data suggest heat is shortened. Young, Dempsey and Myers (35b) observed variable effects. Some animals remained in heat as if nothing had happened, others experienced a short post-copulatory refractory period during which lordosis could not be evoked, and in a third group heat appeared to be terminated.

Closely associated with heat in point of time is a male-like mounting activity which is displayed by approximately 90 per cent of the animals. Its maximum display usually coincides with the begin-

ning of heat (Young and Rundlett, 39). As with the rat, female guinea pigs which are showing this homosexual activity pursue other animals, mount them and display copulatory movements without licking their genitalia afterward. The extent to which mounting occurs varies from animal to animal, but in individuals there is a tendency to consistency from cycle to cycle. The extent of mounting is not related to the length or intensity of heat; in fact, at least two animals have been observed in which mounting activity displayed at 16- to 17-day intervals was unaccompanied by heat. It is not, therefore, an unfailing sign of heat. Furthermore, because it is seen so commonly in normal animals, caution should be observed in regarding it as evidence for a masculinization of behavior following x-ray treatment of the ovaries (Steinach and Kun, 31), or hybridization (Guyénot, Ponse and Wietrzykowska, 32), or as evidence for an inversion of sexual instincts by pre-natally injected male hormones (Dantchakoff, 38).

Investigators have long been aware of the occurrence of estrus shortly after parturition in the guinea pig, and prior to the development of the vaginal smear technique by Stockard and Papanicolaou (17, 19), the time of parturition was generally depended on as a point of departure for investigations of reproductive activity in this species. Oddly enough, though, relatively little precise information was obtained with respect to the frequency of postparturitional heat and its character compared with heat in the non-pregnant animal. Ishii (20) reported it as being displayed within 7 hours after parturition in 18 of 20 animals. He thought of it as being a less vigorous heat, but on the whole of longer duration than normal heat. Tresidder observed copulation in 12 animals immediately after

parturition. Additional data have recently been obtained (Boling, Blandau, Wilson and Young, 39), which indicate that postparturitional estrus is of less frequent occurrence than heat in non-pregnant animals, that the interval between the end of parturition and the beginning of heat is usually less than two hours, and that its average length, 3.5 hours, is less than half that in non-pregnant individuals.

The theoretical possibility that heat occurs during pregnancy in the guinea pig is suggested by Nicol's (33) observation that in two of four pregnant animals typical estrous smears were obtained. The only instance which has come to the reviewer's attention in which there was known to be a willingness to mate is an unrecorded case which occurred in his own colony several years ago. Sixteen days after an artificial insemination which was subsequently shown to have been successful the vaginal membrane ruptured but estrus was not observed. On the forty-third day the animal was found in heat and artificial insemination was accomplished without incident. On the 58th day when the female was again examined, a well advanced pregnancy was detected and on the 71st day one normal young was born. The heat observed on the 43rd day of pregnancy was of normal vigor and mounting was displayed.

The guinea pig is one of the mammals in which heat occurs during lactation (Ishii, 20; Zuckerman, 32), but no observations have been made of its character.

The relationship of ovulation to heat in the guinea pig is quite definite. Although minor variations are encountered, there seems to be no question but that the end of heat is associated more closely with the time of ovulation than with any one vaginal condition (Young, 37), and

that ovulation occurs near the end of heat (Myers, Young and Dempsey, 36). The failure of heat at the time of ovulation is not uncommon, but in no one of 101 non-pregnant animals in which heat was observed and in which the ovarian condition was known was there a failure of ovulation (Young, Dempsey, Myers and Hagquist, 38). In six additional animals in which large follicles developed, but failed to luteinize and rupture, heat did not occur. Because of these observations the suggestion is made that the guinea pig is a species in which heat normally is dependent on ovulation or at least on follicular changes leading immediately to ovulation. The chief need for reservation is that heat is reported in x-ray treated animals (Genther, 31, 34) in which follicular development was incomplete. Unfortunately it is not known that estrogen was the only hormone being produced by these ovaries (Schmidt, 36).

The rabbit

Although the state of heat can easily be recognized in the rabbit and this species has been used widely for investigations of reproductive activity, satisfactory data bearing on the conditions under which estrus is shown are lacking. The response given by the rabbit in heat bears considerable resemblance to that given by the rat and guinea pig. When jumped by the buck she elevates her hind quarters and raises the tail in such a way that the small of the back is depressed (Hammond and Marshall, 25). What would appear to be the slightest stimulus such as fingering the back or the approach of the buck is often sufficient to evoke the heat response (Fee and Parkes, 30; Büttner and Wienert, 35). Does which are not in heat when jumped will squat, arch the back, and draw in the tail between the legs in such a way that copulation is impossible.

Often, too, they will attempt to raise the head and forelimbs in the corner of the cage thereby strengthening the squatting position and better avoiding the attentions of the male (Dr. Paul B. Sawin, personal communication). Aside from this, nothing has been found which would indicate that an antagonistic attitude is taken toward the male when the female is not in heat. The display of homosexual behavior is common.

According to Hammond and Marshall (25) and Fee and Parkes (29) there is no regular estrous cycle and the rabbit will generally mate throughout the breeding season. Recent observations, on the other hand, discredit this older opinion. According to Reynolds (31), Büttner and Wienert (35), and Friedman (38), the periods during which rabbits will copulate are varied and uncertain. Büttner and Wienert suggest that the regularity or irregularity of these periods, as the case may be, depends on the sensitivity of the ovulating mechanism to the stimulus given by the advances of the male. Friedman states that estrous rabbits are obtained with greatest consistency if the choice is limited, not to isolated animals, but to healthy postpartum females, particularly if consideration is given an unfavorable seasonal factor during October and November. The problem is further complicated by the suggestion of a cycle of follicular activity estimated to be about 7 days in length (Shibata, 31; Büttner and Wienert, 35). It is evident, if the rabbit is to be fitted into a comparative picture, that systematic observations are needed which will include attempts to identify the hormonal factors involved, and attempts to correlate changes in ovarian structures with changes in behavior.

There is less uncertainty about other features of estrus. Copulation has no effect, the male is accepted repeatedly.

Interesting observations by Hammond and Marshall (25) cover the periods of gestation and lactation as well. Up to 12 hours after copulation, practically 100 per cent of the animals were receptive. Between the 12th and 30th hours the does began to go off heat and between the 33rd and 39th hours all refused to copulate. After this time increasing numbers copulated, from 22 per cent at the 40th hour to 100 per cent on the 14th day and later. Immediately after parturition all the animals mated, but during lactation the percentage in heat declined progressively and no doe came into heat between the 15th day and the end of the suckling period. Two exceptions were noted. If no more than one or two young were suckled, or if seven young were suckled no more than two hours a day, the lactating adult usually remained in heat. Hammond and Marshall, Reynolds, and Friedman report that pseudopregnant rabbits also accept the male, although with reduced frequency.

It is well known that ovulation in the rabbit depends on copulation. Heat, therefore, does not depend on ovulation or the follicular changes leading up to ovulation, but the presence of follicles above a certain minimum size does appear to be necessary. Büttner and Wienert report that the ovaries in three-fourths of their animals showing heat reactions contained follicles larger than 1.5 mm. in diameter and that in the remaining fourth the size was 1 to 1.5 mm.

In addition to the observations recorded above for the rat, mouse, guinea pig and rabbit, miscellaneous data are reported for a few other rodents. Mating is nocturnal in the golden hamster, ovulation follows in a few hours, there is no postpartum ovulation and a 2- to 4-weeks lactation anestrus occurs (Deanesly, 38). The gray squirrel is similar to the extent

that there is no postparturitional heat and no heat during lactation (Deanesly and Parkes, 33).

Musk rats mate when they are partially submerged in water. Mating depends on the female. If she is not in heat coaxing is without effect, in fact, the male is fought off, but as soon as the female is willing to mate, she squeals and leads him to the water where several matings occur after which they wash themselves (Svihla and Svihla, 31).

In captive porcupines observed by Struthers (28) rutting was evidenced by a pairing of two individuals. After an initial period of indifference to each other the female took the initiative by following the male about the cage and sitting near him when he was inactive. Eventually he became very attentive, and frequently they went through the amusing exercise of rubbing noses. These activities continued for about two days when copulation occurred. It lasted for several minutes after which there was no repetition.

Beyond that brought together in the paragraphs above, there is little if any information about the heat responses of normal female rodents. Eventually generalization will be interesting and undoubtedly of comparative value, but for the present, such an attempt would be unwise if not impossible. We have knowledge of too few species and conspicuous differences are shown by those for which data exist.

The sheep

During the breeding season which varies from one part of the world to another, depending partly on the breed and partly on climatic and nutritional conditions, the non-pregnant sheep comes into heat at about 16- to 17-day intervals. Unlike several of the rodents, in which heat is predominantly nocturnal, it may begin at

any time in the 24-hour period (Cole and Miller, 35; McKenzie and Terrill, 37).

Agreement is general that external signs of heat in the absence of a ram are variable and of little diagnostic value (Marshall, 042; McKenzie and Phillips, 30; Grant, 34; Roux, 36; McKenzie and Terrill, 37). She may eat less than usual, stand apart from the others or even search for a ram. In other cases she may show no indications of heat until teased by the ram when she will stand and allow him to mount. Marked restlessness is not shown. Toward the end of heat a reluctance to stand for the teaser has been found and at this time there may be a preference for a particular teaser.

When not in heat the ewe may jump away immediately when approached by the ram, but more often, according to McKenzie and Terrill, she will stand, allow the male to sniff at the vulva, urinate and then move away quickly when the teasing actions start. At no time is there a strongly antagonistic reaction. The intensity of heat varies during the course of a single period. According to Grant the beginning is sharply demarcated, the end much less sudden. Roux also finds the beginning abrupt, but the end is gradual only in some animals. McKenzie and Terrill report that either end may be abrupt or gradual and that there are no indications one end is more abrupt or gradual than the other.

The average length of heat is anywhere from 27 to 40 hours, the extreme range recorded, 3 to 96 hours. Long heat periods are generally more intense than short ones (Grant, 34). Short heat periods may be experienced near the beginning and end of the breeding season (McKenzie and Terrill, 37), although Cole and Miller (35) found no indication that this is the case. The former authors also state that sterile copulation tends to

shorten the duration of estrus. There is no record of homosexual behavior by normal ewes in estrus, but McKenzie and Terrill observed its occurrence in four ewes beginning about two weeks after daily injections of 200 R. U. Progynon-B were started. One of these ewes appears to have been spayed. In at least two of the remaining three the ovaries were present.

Postparturitional heat does not occur in the ewe (Quinlan and Maré, 31; Roux, 36). Heat during pregnancy has not been observed, but two fairly well authenticated instances of superfetation indicate that occasionally it may be shown. In a case described by A. D. B. Smith (27a) mating is thought to have occurred 28 to 40 days after the previous conception. In a case described by Grant, a second mating is estimated to have taken place about two months after the first. One instance of heat during lactation has been observed by Cole and Miller and they add that the vaginal smear of the lactating ewe indicates that this may be rather common.

The relationship of the ovarian changes to heat in the sheep has been carefully studied. There is agreement among the investigators cited above and Green and Winters (35) in addition, that ovulation occurs during the second half of heat, if not near its end. Furthermore, most have observed ovulation without heat, especially near the beginning and end of the breeding season, but there is less certainty about the occurrence of heat without ovulation. Marshall (01) states that in every case when a sheep was killed after estrus had been observed a corpus luteum was found. Grant reports that not one of the 400-500 mature ewes examined at the abattoir during the normal breeding season failed to show corpora lutea. On the other hand, McKenzie,

Allen, Guthrie, Warbritton, Terrill, Casida, Nahm, and Kennedy (33) state that ovulation did not occur at estrus in 8 per cent of the animals they observed (presumably 141). In the later article (McKenzie and Terrill, 37) it is noted, however, that two ewes which came into heat without ovulation were again in heat 4 and 4.5 days later when ovulation did occur.

The reviewer's interpretation of these results is that the first heat which was unaccompanied by ovulation probably was associated with the presence of one or more large follicles; and that either it was of the prolonged intermittent type caused by a delay in ovulation, or, the follicles responsible for it failed to mature after reaching the preovulatory level and were replaced at the time of the second heat by follicles whose maturation was completed. In either case, the observation could be reconciled with the conclusion that in the ewe heat does not occur without ovulation or at least in the absence of changes which normally lead to ovulation.

The cow

The non-pregnant cow comes into heat at intervals of about 19 to 20 days. According to Hammond (27) the various symptoms are displayed best when a bull or other cows are present. At the beginning of heat the cow becomes restless. She twitches her tail frequently and often raises it. When at pasture she usually does not continue to feed, but wanders about the field and frequently goes off by herself or with another cow which she rides. When the bull attempts to mount her she will stand still and not run away as happens when an animal is not in heat. A cow in heat frequently lowers the hips and small of the back and raises the tail end. She will also frequently play with

the bull by horning him or will stand and lick him and when separated from other cattle will "blar." There is usually a short period when the cow is coming into heat and a rather longer period toward the end when the symptoms are less marked; during the remainder of the period, no difference in intensity can be observed.

According to Hammond the duration of heat averages 17 hours, range 6 to 30 hours. Weber (10-11) observed that cows which showed an intense heat usually had longer heat periods than those in which the manifestation of heat was slight. He also states that the length of heat is not affected by copulation.

Cows in heat commonly jump other cows and bulls. This behavior reaches its extreme expression in nymphomania when the "whore-cow" not only mounts other cows and bulls repeatedly but may even attempt to mount other species including man (Williams and Williams, 21). When this pathological condition exists she perhaps "blars" more frequently than when she is in heat and in such a way that the call can scarcely be distinguished from that of the bull. As a rule such a cow will copulate at any time, but there are exceptions in which willingness to accept the bull is not continuous.

There is no postparturitional heat in the cow. The first heat occurs at a variable time after parturition, if the cow is milked, usually between 3 and 7 weeks later (Chapman and Casida, 37; Hammond, 27; Weber, 10-11). After this time heat occurs regularly. If the calf is suckled, the first heat may not occur until after three months. Occasionally cows show a return of heat after conception, but its appearance is irregular and usually it ceases to recur after the 3rd or 4th month, although rarely it is seen up to the 7th or 8th month (Williams and

Williams, 21; Strodthoff, 22; Hammond, 27).

Ovulation occurs about the end of heat (Williams and Williams, 21; Strodthoff, 22) or shortly after the end (McNutt, 24; Hammond, 27). According to Strodthoff who examined the ovaries by rectal palpation, either may occur without the other.

The sow

In non-pregnant sows heat occurs throughout the year at intervals of approximately 21 days. According to Corner (21) the

duration of estrus is commonly 3 days, during which time the sow exhibits excitement in the presence of the male, with ready acceptance of coitus. If no male is present, the sow will follow other females about the pen, sniffing at their genitals and frequently imitating the sexual act by "riding" the others. In a larger herd without boars the female in heat will often be found in a separate group apart from the others, where for hours at a time the exhibition of the sexual urge continues until at the end of 3 days, or occasionally longer, it subsides.

McKenzie (26) also calls attention to the restlessness of the sow which is in heat, but adds that some sows go through estrus without exhibiting restlessness. According to Altmann (39) the peak of activity occurs toward the end of estrus, and during estrus the animal is less combative. The heat period is not terminated or shortened by coitus (Corner, 19).

Data bearing on the time of the first heat postpartum, heat during pregnancy and heat during lactation are inadequate to give finality to the conclusions they suggest. As in the other ungulates for which information exists, there appears to be no postparturitional heat. According to Struve (11) the interval between parturition and the first heat is 4 to 9 days. According to Marshall and Hammond (25) the interval is between 30 and 60 days. Heat during pregnancy is un-

common if it occurs at all (Corner, 21). The possibility is suggested, however, by the fairly well authenticated report of a superfetation (A. D. B. Smith, 27b). The reviewer has found only one reference to the subject of heat during lactation. Marshall and Hammond state that as a rule the sow which is suckling a litter only rarely comes into heat until 5 to 6 days after the young are weaned.

There are few references to the ovarian changes and heat. It seems clear from Lewis' (11) data and the articles by Corner that ovulation usually occurs on the second day and therefore during the second half of heat. Whether or not ovulation occurs without heat is not known. From Corner's (19) statement that the ovaries of all sows killed during heat contained mature or recently ruptured follicles, it may be assumed that heat is usually if not always accompanied by ovulation.

The mare

During the breeding season which may extend throughout the year when animals are maintained on a reasonably high plane of nutrition, heat in the non-pregnant mare recurs every 21 to 23 days. The estrous responses are described briefly by Satoh and Hoshi (33) and by McKenzie and Andrews (37) in a preliminary communication. They seem to be best observed in the presence of a stallion.

During the diestrus, according to McKenzie and Andrews, the mare resists any attempt of the stallion to approach or tease her by kicking actively if he approaches the hind quarters or by striking or even attempting to bite if he approaches from the front. As the period of heat nears, the mare still tries to repulse the stallion by kicking, but she does not show the higher degree of resistance displayed earlier in the diestrus. The first day of heat the mare no longer repels advances of

the stallion. She stands quietly as he approaches, and as he teases by smelling and gently biting her over the withers she raises her tail, but appears little interested in him. Urine may or may not be passed. After she has been in heat a day or more, she still raises her tail when the stallion begins to tease her, but she now stands quietly and permits the stallion to mount without difficulty. The vulva undergoes rhythmic contractions. An increase in the intensity of the reactions roughly parallels the growth of the follicles and and maximum receptivity is reached shortly prior to or following ovulation. Soon afterwards the mare passes into a condition of mild receptivity comparable to that displayed on the first day, if not into the actively resistant condition of the diestrus. Once heat has begun willingness to accept the male is not always constant. Satoh and Hoshi (33), McKenzie and Andrews (37) and Day (39b) have noted that the estrous responses may be given intermittently with ovulation at the end. Andrews states in a personal communication that the percentage of pregnancies in mares displaying this type of heat seems to be normal. There is no indication that homosexual behavior is ever shown.

The length of heat is reported to vary from 1 to 27 days, but to average 5 to 7 days (Aitken, 27; Schtschjekin, 30; Mirskaia, 35; McKenzie and Andrews, 37). According to Aitken and Schtschjekin breeding has no effect on its length.

In the mare what is known as the "foal heat" occurs relatively soon after parturition but not as soon as the postparturitional heat of rodents, seals (Elliott, 84; Rowley, 29), and certain insectivores (Brambell, 35; Brambell and Hall, 36, 39). According to Schtschjekin this heat may occur any time from the 5th to the 30th or 40th day, although more animals

come into heat on the 9th to 11th day than at any other time. In the observations by McKenzie and Andrews, the mean length of the interval was 7.25 days, range 2 to 12 days.

Heat during pregnancy in the mare is of occasional occurrence (Marshall and Hammond, 25). Satoh and Hoshi are more definite. During 1929, 5 of 71 pregnant animals showed signs of heat; during 1930, 3 of 92; and during 1931, 6 of 96.

Numerous observations bear on the relationship between changes in the ovaries and heat. Agreement is general that ovulation occurs near the end. Ovulation without heat has been found in normal appearing mares (McKenzie and Andrews, 37; Satoh and Hoshi, 33) and in mares injected with gonadotropic hormones (Day, 39a). Most interesting, however, because the mare is the only spontaneously ovulating species thus far described in which it has been encountered so commonly, is the occurrence of heat in the absence of ovulation (Satoh and Hoshi, 33; McKenzie and Andrews, 37; Zavadowsky and Goldberg, 37; Day, 39b; and Day, 40, in the pony mare). McKenzie and Andrews state that an occasional female was receptive for a day during the diestrus and that in some mares there were no detectable follicles. Satoh and Hoshi refer to two types of heat without ovulation. One is of short duration and of weak intensity, and a follicle never develops completely. The other type is normal in appearance and duration and may be found about the end of the breeding season. A larger follicle is always found, but it degenerates instead of maturing. Zavadowsky and Goldberg assume that the sterile matings of frequent occurrence toward the end of the breeding season can be explained by the failure of ovulation.

Completion of the description of the

mating behavior of rodents and ungulates permits a brief comparison of the more noticeable features. In the opinion of the reviewer, such a comparison reveals at the outset that the similarities in the fundamental features of the behavior and the phenomena associated with it outnumber the differences. The chief differences appear to be the common occurrence of postparturitional heat in many rodents and the greater length of heat in the ungulates. The posture simulating a lordosis is assumed by species in both groups, restlessness is common, homosexual behavior is displayed by certain species, and, except for the rabbit, ovulation is spontaneous and usually occurs during the second half of heat, if not near the end. Whether or not these similarities are the expression of comparable heat-inducing mechanisms cannot be decided until the experimental procedures tried with success on rodents can be tested on ungulates.

The carnivores

Of the carnivores for which data exist, all except the dog show a heat behavior which in one way or another is more elaborate from the standpoint of display than that encountered in the other orders.

The behavior of the cat has been described by Van der Stricht (11), Bard (34, 36, 39), Greulich (34), and Maes (39, 40a). Bard's (39) description is quoted:

Feline estrual behavior may be divided into *courtship activities* and the *after-reaction*. The former includes playful rolling, excessive rubbing, a curious low vocalization (calling) not heard at other times, and crouching and treading. The estrual crouch is a most specific posture. Resting on chest and forearms with pelvis and tail elevated the animal tends to execute treading movements of the hindlegs. It is in this posture that the female accepts the male. Intromission is almost always signalled by a loud cry or growl which suggests anger or pain; some

females utter a piercing shriek. The after-reaction, which follows any mechanical stimulation, penile or artificial, of the distal vagina consists in more or less vigorous rolling, sliding, rubbing, squirming and licking. Most animals will not again accept the male until the after-reaction has run its course. No trace of this response can be elicited by vaginal stimulation in cats which are in anestrus.

Normally cats go into heat two or three times a year. The intervals are irregular. The duration of estrus varies greatly from individual to individual and in the same individual from time to time; the average lies between three and ten days. The best criterion of full estrus is of course successive acceptances of the male, but many cats display marked courtship activities for a day or more before they will permit a male to mount. Some cats engage in courtship activities quite spontaneously; for example, they crouch and tread even when isolated from all other animals and left quite alone. Others do not show the behavior unless they are in the presence of a male or receive some stimulation of the external genitalia or of the skin surrounding the vulva. When a cat is in estrus she responds to light rubbing or tapping of the genital region by crouching and treading or if already in a crouch, by treading. Many females, but not all, show this response when the loose skin of the nape of the neck is grasped to mimic the action of the male who on mounting always holds the female in this fashion.

According to Greulich (34), the periods of rolling are interrupted by intervals during which the animal licks the vulva and rubs itself vigorously, especially its head and back, against any suitable available object. This period of activity is followed by one during which the animal lies quietly on its side, often purring softly and opening and closing its front paws—behavior which is usually interpreted as indicating a feeling of contentment and well-being. If the animal had only just come into heat, or if it had been stimulated only once or twice, it would ordinarily submit willingly to a repetition of the procedure within 15 minutes to a half-hour after the beginning of the inactive phase just described.

Ovulation depends on the stimulus of copulation and terminates heat, but not

until 2 to 5 days have elapsed (Longley, 11; Courrier and Gros, 33; Liche, 39). If the cat is left with the male during this interval between the first copulation and the end of heat, many other copulations occur. If there has been a lack of service, heat may be prolonged to 10 days or more (Liche). Ovulation is said to occur from less than 25 to as long as 54 hours after copulation (Courrier and Gros; Greulich; Liche; Dawson and Friedgood, 40).

The ferret is another carnivore in which the heat period is terminated by copulation provided ovulation occurs. Otherwise, heat may last as long as four months (Marshall, 04a, 04b; Robinson, 18; Hammond and Marshall, 30). Another peculiarity of the ferret is the prolonged copulation during which the female is tightly clasped by the male and rolled around as though they were engaged in a wrestling match. According to Hammond and Marshall, it may take an hour or more after the first attempt is made before copulation is effected, and the actual time of union may vary from 5 minutes to 2 hours, 55 minutes. When coitus is successful, ovulation follows in about 30 hours (Hammond and Walton, 34).

In the otter copulation is prolonged as in the ferret and accompanied by a vocalization encountered thus far only in the carnivores. Cocks (81) describes a case in which a pair mated in the water July 17th, the female chattering loudly and whistling in a peculiar way all the while. They remained thus for about an hour, swimming the entire time. August 12th they again paired in the water. They remained together on this occasion between an hour and an hour and a half.

Wight (31) describes the heat and mating behavior of the skunk in which many of the elements which are apparently common to the carnivores can be recognized.

He states that the proestrus is indicated by complaining cries which presumably result from the male's attempt to copulate. In each attempt, the male seeks the female and engages in a struggle which appears ferocious, but which in reality is little more than a gesture. Each attempt varies from 5 to 10 minutes and terminates when the male voluntarily leaves the female without having completed copulation. During estrus an initial struggle accompanied by a massaging or titillation by the male is quickly followed by assumption of the receptive attitude which involves an elevation of the tail. In a case Wight observed, successful matings were made over a 51-hour period. They varied in duration from 5 to 20 minutes. During the last mating the female began to growl before being released by the male. From this time on he was constantly on guard and moved away to preen himself. The female also preened herself; the only time she did so after copulation and it apparently indicated the end of heat.

The heat behavior of the dog presents many features which differ, not only from the other carnivores, but also from the other mammals. The essential details are taken from Evans and Cole (31).

At the beginning of proestrus as determined by the escape of blood-tinged fluid from the vulva, males are invariably attracted. While we do not know whether persistent following would take place at so early a period, this soon becomes the case, even though during most of the proestrus the female is actually hostile to the attentions of males. A day or two before the close of this epoch, i.e., a day or two before she accepts coition, a marked change in her demeanor is noticeable. At this time she will then endeavor to attract the attention of males by quick darting movements and stamping of the forefeet. During the first two days of active oestrus a maximum expression of sex desire on the part of the female is evidenced. Postural invitation to coitus is unmistakable. There is then a gradual recession of her interest from day three to the end of oestrus. During

the last day or two of oestrus, repellent actions on her part are usually evidenced, though with persistence on the part of the male, copulation is finally permitted.

Elsewhere they state that the length of estrus in 12 animals varied from 4 to 13 days, that ovulation is spontaneous and occurs early in estrus, usually on the second day, and that the dog continues in heat for somewhat more than a week after ovulation. With respect to spontaneous ovulation and the length of heat after ovulation, the dog and possibly other Canidae such as the silver fox (Rowlands and Parkes, 35) differ from the cat and ferret. In these species ovulation is not spontaneous and heat is terminated about the time of ovulation.

The relationship between the time of ovulation and heat in the dog differs from that in other spontaneously ovulating mammals. In every mammal of this type for which data have been found, except possibly the mouse, ovulation occurs during the second half of heat, if not near its end. If there is a failure of ovulation after the pre-ovulatory changes have begun, as in the cow and horse, heat persists as nymphomania (Williams and Williams, 21). Normally and pathologically, therefore, in spontaneously ovulating mammals the end of heat is closely associated with ovulation. Yet in the dog the temporal relationship is different, ovulation occurs near the beginning of heat and heat continues for a week or more. The implication is that the heat-inducing mechanism in the dog is different from that in other spontaneously ovulating mammals. A systematic investigation of the species, and of one or more other Canidae, would be of interest.

From the incidental data already cited and other information, it would seem that the heat period in carnivores is generally longer than that in rodents and ungulates.

In addition to the data already given for the cat, ferret, skunk and dog, the tiger in zoological gardens is thought to have a heat period of about 8 days and that of wolves, jackals and foxes in zoological gardens is said to last 7 to 9 days (Heape, 1900). Rowlands and Parkes (35) state, however, that heat in the silver fox lasts only 3 to 4 days.

No suggestion has been found that homosexual behavior is ever displayed by the carnivores.

No data have been found bearing on the possibility of postparturitional heat except for Robinson's (18) reference to 2 ferrets which were in heat after parturition. Doubt is cast on this suggestion of postparturitional heat by Hammond and Marshall's (30) statement that the generative organs of a suckling ferret were in the anestrus condition 17 days after parturition and that a second animal whose young were killed immediately after birth did not begin to come on heat until 9 days later. The only instance of heat during pregnancy in an untreated carnivore is one recorded for the mongoose on the 24th day (Frere, 29). Its occurrence under experimental conditions following the injection of a pregnancy mare serum preparation into 3 pregnant cats is described by Windle (39). No evidence has been found that heat is ever displayed during lactation.

The occurrence of ovulation about 30 hours after copulation in the ferret and about 24 to 30 or more hours after copulation in the cat has been mentioned. Enders (40) suggests that in the mink, too, ovulation follows copulation or a similar stimulus in from 42 to 52 hours. How generally ovulation depends on copulation in carnivores other than the Canidae is not known. The prolonged copulation in the otter and the repeated copulations apparently indulged in by the skunk

(Wight, 31) and mongoose (Frere, 29) suggest that ovulation may also depend on the stimulus of copulation in these species. Correlation of follicular development with heat and copulation has been made for the ferret (Robinson, 18), dog (Evans and Cole, 31) and cat (Dawson and Friedgood, 40).

If the dog is excepted, the available information bearing on the heat behavior of the carnivores can be summarized in the form of several generalizations which must necessarily be tentative. Heat appears prior to the time of the ovarian changes which lead directly to ovulation and is generally long. Its display tends to be more elaborate than in the other groups. Copulation does not seem to shorten heat except as it stimulates ovulation with which the end of heat is associated. Copulation is frequently very much prolonged or at least repeated. Compared with the rodents and ungulates the interval between copulation and ovulation is long. Homosexual behavior has not been reported.

The infra-human primates

Investigations of sexual behavior in infra-human primates went through an initial period when the opinion was held that in most representatives of this group, there is no recurrent period of heat, that females will accept the male whenever they are given the opportunity. This opinion is elaborated on most fully by Miller (28, 31). It appears to have had its origin in the report of sexual behavior given by Hamilton (14) for 18 macaque monkeys and 2 baboons, by Montané (16) for a pair of chimpanzees, by Hartman (28) for macaques and by Fox (29) for the orang-utan. Observations reported by Tinklepaugh (28) for *Macacus rhesus* might also have contributed to such an interpretation.

The necessity for modifying this conclusion soon became apparent because many investigators presented convincing evidence for the existence of cyclic periods of heightened sexual desire not only in the lower primates, such as the lemuroid, *Galago senegalensis moholi* (Lowther, 40), but also in the higher non-human primates. Gear (26) states that female *Chacma* baboons will not tolerate sexual advances of the males during the diestrus or metestrus, but that they permit and even solicit their overtures during the period of genital enlargement. Zuckerman (30, 32) confirms this conclusion to the extent that the desire for mating is greatest when the swelling of the sexual skin is the greatest, but he differs with respect to the willingness to mate during the diestrus. According to him, baboons seldom mate during the quiescent phase of the sexual skin, but a female is rarely observed to refuse the male. The grey-cheeked and sooty mangabey, the Moor monkey (*Macacus maurus*), and the pig-tailed macaque (*M. nemestrina*) appear to be more sexual than baboons during the quiescent phases of the perineal region. Nevertheless, the desire to mate is strongest at the height of the swelling, thus indicating a periodicity in these species. The same author agrees with others who have observed *Macacus rhesus* under laboratory conditions, that members of this species copulate at all times, but he is also convinced that mating is more frequent when the sexual skin is active. Hartman's agreement with this conclusion, and correction of his earlier opinion, is indicated by the statement in Ball and Hartman (35) that sexual excitability increases just before ovulation and falls thereafter, even though the drop is not usually so complete as to mean consistent refusal to mate. Periodicity of sexual behavior is also indicated for the Java macaque

(Spiegel, 30) and for the bonnet macaque (Hartman, 38). With respect to the latter species, Hartman states that the bonnets studied in the Carnegie colony are more restricted in their periods of receptivity than rhesus females. However, in view of data recently accumulated by Carpenter (in press), it is doubted that the bonnet macaque displays an estrus which is more sharply limited than that of *Macacus rhesus* under free range conditions. An article by Hamlett (39) contains no observations of behavior, but from his examination of the vaginal contents at various stages in the cycle he concludes that the species of *Cebus* monkey studied appear to copulate only at a definite time in the cycle. The existence of a definite estrous period in other New World monkeys is clearly indicated by the observations of Lucas, Hume and Smith (27) on the marmoset and by those of Carpenter (34, 35) on howler and red spider monkeys.

The best controlled observations on the great apes have been those on the chimpanzee by the Yale University group. They provide a substantial basis for the conclusion, suggested by Köhler (26) and Fox (29), that although copulation may be accomplished at any time during the cycle, it apparently is more interesting to both animals during the periods of genital swelling (Tinklepaugh, 30, 33; Elder and Yerkes, 36; Yerkes, 39a; Yerkes and Elder, 36).

The apparent explanation for the failure of early observers to detect the periodic change in sexual desire shown by infra-human primates is that proper allowance was not made for the influence of certain nonsexual factors such as individual characteristics of the consorts, social relations and environmental circumstance which tend to obscure the manifestation of cyclic changes in reproductive behavior within

this group. The influence of certain of these factors is obvious from the observations on the behavior of female chimpanzees in the presence of dominant males (Sokolowsky, 23; Schultz and Snyder, 35), but their importance is especially emphasized by Zuckerman (32), Yerkes (39a) and Yerkes and Elder (36).

After citing an experiment in which a reasonably homogeneous group of chimpanzees was tested, Yerkes and Elder state:

... we may safely assert that when mating experiments are conducted with a homogeneous group of subjects and important factors are varied singly, the copulation distribution is transformed by limitation to the mid-third of the sexual cycle. This we have ventured to designate as the period of oestrus in chimpanzee. By varying the nature of the social relations among consorts, the maximal frequency of copulation may be shifted. ... Thus, for example, if individuals unacquainted, uncongenial, or hostile be used as mates, copulation tends to extend into the first third of the cycle, and it may for certain consorts become coextensive with the cycle. For it clearly appears that receptivity may be completely overshadowed by the dominance and aggressiveness of the male or by the timidity and defensiveness of the female. Consequently, if in an experimental study of mating behavior, with interest in the existence, strength, and relations of sexual desire and receptivity, subjects are chosen irrespective of their social relations, developmental status, and sexual experience, extremely diverse and highly variable results should be expected, and it may very well appear that copulation is not limited to any phase of the sexual cycle.

... our data establish that in a given instance environmental stimuli may determine the mating pattern, either inducing positive response when it would not otherwise occur, or inhibiting it despite strong sexual desire in both consorts. ... It appears similarly that such social factors as strangeness, hostility, devotion, may compete with primary physiological factors and in some instances dominate.

The importance of the physical characteristics of the consort is discussed elsewhere (Yerkes, 39a):

The relationships exhibited by the table [estimates of age, physical and sexual vigor, penis length, and intelligence for 3 males] in conjunction with details of observation ... strongly support the generali-

zation that the sexual acceptability of M to F tends to vary directly with vigor, penis length, and copulational time and thrusts, and inversely with degree of sexual selectiveness, dominance and aggressiveness. . . . it appears that female preference in mates is dependent largely upon the physique and sexual behavior of the male.

Individual variations among males with respect to the influence of the sexual status and traits of the female are extreme. One male, for example, may consistently refuse to mate with a given female, or he may accept her only for a few days—almost certainly those approximating the time of ovulation . . .—during the normal sexual cycle. Another male, by contrast, may eagerly accept or even insistently solicit the same female throughout the three phases of genital swelling, and even when her sexual receptivity is very slight. Similarly, [a female consort may consistently refuse one male and in the next minute eagerly mate with another. . . . In many of these cases of anomalous sexual behavior the essential condition seems to be social incompatibility, but this of course may trace to the influence of physique, of immediate behavior, or of preference for another mate over the one at hand.

Such a shifting of the frequency of copulation beyond the period of heat is unknown in the lower mammals. Its nearest counterparts are seen in the rat in which a more intense response is often given to an aggressive male (Miller, 11; Stone, 22; Hemmingsen, 33; Ball, 37a), and in the ewe toward the end of heat when there may be a preference for a particular teaser (Roux, 36).

Another characteristic of primate behavior which is not encountered in the lower mammals, and which tends to obscure the picture as far as the definition of an estrous period is concerned, is the use of the sexual responses as a means of obtaining material advantages such as food or protection from enemies (Hamilton, 14; Zuckerman, 32; Maslow, 36; Gillman, 39). Bingham (28) has added to this list the tendency to show off sexually in the presence of interested spectators.

The characteristics of female behavior during the period of heightened sexual

desire have been described for the howler monkey (Carpenter, 34), the rhesus monkey (Carpenter, in press) and the chimpanzee (Yerkes and Elder, 36; Yerkes, 39a). Carpenter states that the external genitalia of the receptive howler female cannot be distinguished from the genitalia of non-receptive animals. Estrous females appear to be identifiable in the wild by their behavior during 4 or 5 days of the receptive period. They approach males in their group, display rhythmic tongue movements and assume provocative postures. In addition the female may lick the face and hands of the male. After copulation she may take a position on her back and roll several times from side to side. The female which has just mated also tends to remain closely associated with the male for several hours, or even a day or more, during which time a number of copulations usually occur. Subsequently, if the first male becomes satiated, which generally happens, the female becomes the consort of a second highly motivated male. The possibility of sexual activity outside of the estrous period cannot be excluded. Two observations were made which suggest that copulation occurs sporadically without repetition and without close association of the female and male.

Some of the most interesting data bearing on primate sexual behavior are contained in a field-study of *Macaca mulatta* which Dr. Carpenter has kindly permitted the writer to see in manuscript. Evidence is presented indicating that under the free ranging conditions on Santiago Island the estrous period is much more sharply defined than has previously been assumed from observations of the rhesus monkey under laboratory conditions. It lasted an average of 9.2 days with a range from 4 to 15 days and an average deviation of 2.90 days for 40 females who showed 45

estrous periods. The length is assumed to be regulated in part by physiological factors, but it is postulated that socio-economic factors such as the sexual capacities and dominance characteristics of the male consorts, the presence of only one estrous female in the group, the intragroup dominance status of the female, strong attachments between specific males and females and "habit" perseveration supplement the physiological factors in lengthening or shortening estrus. Carpenter calls the extended behavioral estrus of females caused by one or more of these factors a "perseveration effect."

The onset of estrus is estimated to have a rapid rise in intensity, but the decrement at the end is more gradual. The peak of excitement is thought to occur on the second or third day. During the period of heightened sexual desire there is an increased general activity which is accounted for in part by the female's greater aggressiveness as she ascends the dominance scale. An estrous female in the initial phase of heat leaves her normal subgroup, and in the face of numerous vicious attacks by the males in the large group, approaches them, assumes a crouching posture and performs invitational gestures until one or more responds. She may then express intense sexual excitement by copulation, described as a series of mountings with intromission and several piston thrusts which is terminated by ejaculation, by rapid flexion and extension movements of the dominant hand and arm and by sham attacks on nearby females and young. An association is established between a receptive female and the male of the group with whom she is copulating which may last several days. The females observed by Carpenter had associations with an average of three males in each estrous period. During these associations the male and female

are never more than a few yards apart, grooming is more persistent than during the diestrus and copulation as described above may occur three or four times a day. Estrous females do not always remain in their indigenous groups. Four of forty animals were observed to leave their groups and copulate with males in other groups. Following estrus the female remains in the same group, but she is less closely associated with males, the consort relationship ends and she again becomes a part of the cluster of females and young. Mounting with intromission was seen outside of estrus, but there were no persisting consort associations and such observations may have been of females just beginning or terminating a period of receptivity or of females seeking to avoid an attack or as a means of gaining some end. Data bearing on the relationship between ovulation and estrus have not yet been obtained, but a close association is indicated by Hartman's (32) statement that the rhesus monkey is much less ardent sexually during the summer season of anovulatory cycles. Homosexual behavior is reported as it had been previously by Maslow (36).

In the chimpanzee the willingness to mate is represented as gradually waxing, continuing at a maximum for a few days and then suddenly disappearing after ovulation. The tendency of the fully receptive female is to rush to the male and prostrate herself before him (Yerkes and Elder, 36; Yerkes, 39a). In addition these investigators list the anticipatory behavior while preparations for a mating experiment are in progress, the manner of presentation and the degree of coöperation in sexual union, and the efforts of the female to attract the attention of the non- or slightly responsive male by posture, gesture, vocalization and playful antics. Of frequent diagnostic value is the greater

friendliness displayed by some animals toward human observers. Among the animals themselves a change in the dominance-subordination relationship as measured by a food incentive is often observed (Yerkes, 39b, 40; Crawford, 40). Homosexual behavior is described (Köhler, 26; Bingham, 28; Yerkes, 39b), but Yerkes notes that the animals he studied, instead of mounting their companions as cows, sows and guinea pigs do, were mounted. The writer, on the other hand, has recently seen a female who had just presented mounted by another female with a maximal swelling in a manner which simulated male behavior in every detail except for the absence of the thrusts characteristic of normal copulation.

When the literature bearing on sexual receptivity during pregnancy is reviewed, it seems clear that sexual desire, if it is displayed at all, is exhibited by the pregnant female only during the first month or two of the gestation period (Ball, 37b, for *Macacus rhesus*; Zuckerman, 30, and Hartman, 38, for the bonnet macaque; and Zuckerman, 30, for the baboon). Zuckerman's statement, that a pair of pig-tailed monkeys copulated freely during the pregnancy of the female, has not, as far as the reviewer can ascertain, been confirmed or contradicted. In the chimpanzee mating has been observed throughout all or most of pregnancy (Montané, 16; Bingham, 28; Tinklepaugh, 33). Yerkes (39a) discusses the problem and concludes tentatively, "that pregnancy receptivity is an artifact, due to the reflection by the female of the sexual dominance of her consort."

The differences between the heat behavior of non-human primates and lower mammals can now be considered. Con-

spicuous and important is the extent to which non sexual factors such as fear, the desire for food or the desire to "show off" are dominating stimuli. Equally prominent are the individual characteristics of the members of a pair. Likes or dislikes which may be traceable to social incompatibility or peculiarities of physique appear to go far in modifying the response which would be expected if only the physiological status of the animals were involved. In the lower mammals, the dominance of a male may be decisive toward the end of estrus when the responses are normally difficult to elicit, but there is no record that any amount of aggressiveness will lead to mating when the female is physiologically unprepared for mating. The non-human primates appear to be the only infra-human mammals in which the time of copulation can be shifted outside the limits of the estrous period by psychological or environmental factors.

In this respect they would seem to bridge the gap between the lower mammals in which receptivity is displayed only at the time of heat and the human female. Interestingly enough, the change may have taken place within the Order. There appear to be primates such as the baboons, the rhesus monkey under free range conditions, and certain of the New World monkeys in which the periodicity of sexual desire is clearly evident. In others such as the rhesus monkey, under laboratory conditions and the chimpanzee the limits of the receptive period are less sharply defined, but upon careful observation cyclic changes in the degree of receptivity are seen.

(To be concluded)



HOOK PATTERNS ON THE ACANTHOCEPHALAN PROBOSCIS

By HARLEY J. VAN CLEAVE

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AMONG the worms which have adopted the parasitic mode of life, no group has abandoned the paths of independent existence more completely than the Acanthocephala. They are so perfectly adjusted to parasitic habits that in normal development after hatching no individual ever passes even a brief interval outside the body of some host creature. Females, dwelling in the intestine of a vertebrate, discharge the fertilized eggs into the lumen of the host intestine. When these eggs, each bearing a developing embryo, reach the exterior along with the intestinal wastes of the host, even hatching is contingent on the egg being swallowed by some suitable animal. So far as known, this first host is always an arthropod in whose body the embryo becomes liberated from its shells. Within the body of this first host, development never proceeds beyond a certain point. During the sojourn in the arthropod, the young worm undergoes conspicuous metamorphosis wherein the beginnings of all organs characteristic of the adult acanthocephalon are laid down. It is during this residence in the arthropod host that the proboscis, which is the subject of this article, makes its appearance. The attainment of full growth and sexual maturity for the larval acanthocephalon is deferred until the sheltering arthropod is devoured by a suitable species of verte-

brate in whose intestine the adult worm spends the remainder of its life.

As an accompaniment of such complete adjustment to parasitism, every member of this group has lost all traces of organs and systems reminiscent of independent life. They possess no organs of locomotion, no digestive organs, no highly specialized sensory apparatus and most of them lack all special excretory mechanisms. In fact, the body becomes little more than a sac for sheltering the reproductive organs and a proboscis for maintaining hold on the host tissues. The elimination of so many features, leaves a body of monotonous form with relatively few avenues available for expression of taxonomic characters.

In spite of this drastic reduction in number of morphological features available for reflecting taxonomic differences, more than 300 species representing 58 genera were listed by Anton Meyer (1932-33) in his monograph on the group, and many significant contributions have appeared in the literature since that date.

The proboscis, a hook covered introvert, is the most distinctive organ in the Acanthocephala. Its form and the arrangement of its hooks reflect specific and generic differences more readily than any other single structure, yet previously no attempt has been made to present an analysis of the tendencies toward diversification in the arrangement of the probos-

cis hooks. Of the many diverse types of proboscis which have been described, each has been treated as a specific entity, as though it were a thing in itself without genetic relationships to other patterns. However, much of the evolution of the group is clearly reflected in the diversification of the proboscis and its armature.

In a limited extent, taxonomists have acknowledged this fact, for hook arrangement has always been considered as of great significance in taxonomic descrip-

some species, individual variation is practically unknown, while in others there are wide limits to the number of hooks as well as to their arrangement on the proboscis. Since the hooks are laid down in definitive form and number early in larval life and usually, within reasonable limits, the form and relations remain constant throughout the life of the individual, the taxonomic characters provided by the hooks reveal few growth changes. Within relatively close limits number,

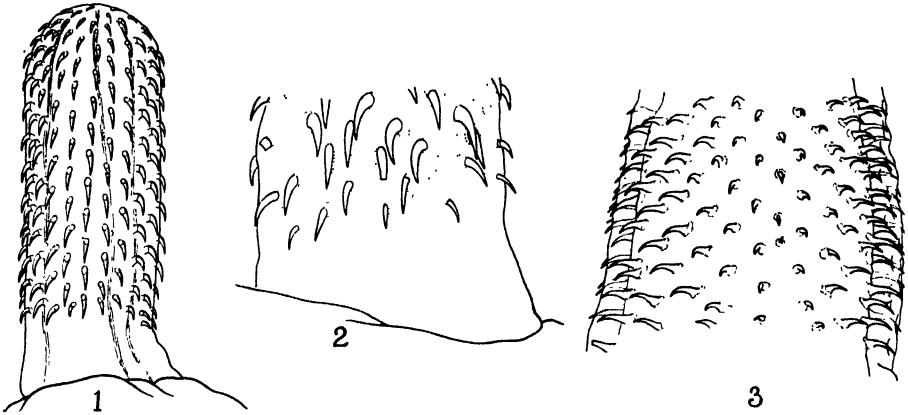


FIG. 1. PROBOSCIS OF *ACANTHOCEPHALUS DIRUS* SHOWING TYPICAL, QUINCUNXIAL ARRANGEMENT OF THE HOOKS WITH LITTLE REGIONAL DIFFERENTIATION (After Van Cleve)

FIG. 2. BASE OF THE PROBOSCIS OF *ACANTHOCEPHALUS RANAE* SHOWING ABNORMAL HOOK ARRANGEMENT ACCOMPANYING THE OCCURRENCE OF AN ODD NUMBER OF LONGITUDINAL ROWS OF HOOKS (After Lühe, 1912)

FIG. 3. BASAL REGION OF A PROBOSCIS OF *CENTRORHYNCHUS* SHOWING DISINTEGRATION OF PATTERN OF ARRANGEMENT INVOLVING ONE HOOK OF COMPLETELY REVERSED ORIENTATION

tions. Diverse systems for designating hook arrangements have been devised in the more than two centuries that these worms have been studied. Some of these systems have been discarded and from time to time other systems have been proposed. Rarely have the suggested schemes been based on any realization of evolutionary changes modifying a simple basic pattern into the diverse expressions of present day forms.

The degree of consistency in pattern of arrangement and in numbers of proboscis hooks is not fixed in equal degree in the various species of *Acanthocephala*. In

form, and size seem to be controlled in practically all species by the hereditary mechanism and can not be subject to direct influence by other factors.

In its most generalized form (Figs. 1 and 4) the proboscis is provided with hooks that are arranged in radial symmetry, with the apex of the proboscis as the center from which regularly ordered rows radiate. Alternating check rows form a pattern that has been commonly referred to as "quincunxial" arrangement. The form of the proboscis is so regular and the pattern of its hooks is so specifically constant in these examples of radial

symmetry that there is little challenge to analyze the monotonous pattern. But even in a proboscis showing radial symmetry not all of the hooks are of identical form and size. There is very commonly progressive axial change in form and size of hooks at the two extremities of the proboscis. Here they are usually more slender and less sharply recurved than in the mid-region. The exact pattern of axial graduation is often distinctive for all members of a species. From this slight axial differentiation as a start, some of

series of both longitudinal and cross rows, but these rows are alternating in staggered fashion (Fig. 1) so that the members of alternating cross rows fall into the same longitudinal rows and *vice versa*. This geometric arrangement makes it convenient in the study of whole mounts to follow diagonal lines of hooks in counting the longitudinal rows visible on one lateral face of the proboscis. In the writings of nineteenth century workers there is still confusion in the interpretation of their descriptions, whether they were

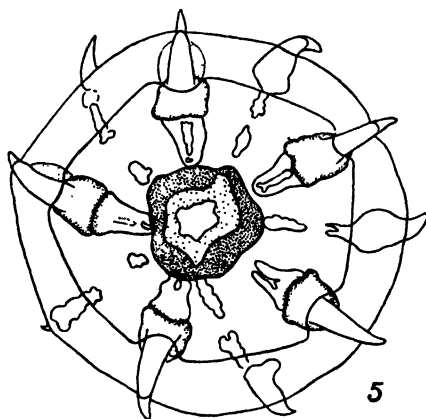
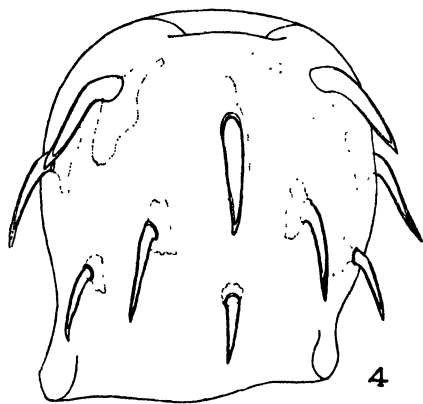


FIG. 4. PROBOSCIS OF *NEOECHINORHYNCHUS CRASSUS* IN SIDE VIEW. (Redrawn from Lynch, 1936)

Example of a simple proboscis with only three circles of hooks

FIG. 5. END VIEW OF AN ABNORMAL PROBOSCIS OF *NEOECHINORHYNCHUS VENUSTUS* HAVING FIVE INSTEAD OF THE NORMAL SIX HOOKS TO EACH CIRCLE (Redrawn from Lynch, 1936)

the most conspicuous zonal specializations have their origin as shown in forms like *Corynosoma* (Fig. 9) and *Centrorhynchus* and *Mediorhynchus* (Figs. 12 and 13).

In attempting to analyze the factors that might be responsible for perfect radial symmetry, either a single factor or a perfectly integrated series of factors might be invoked, for other than the axial graduation in size there is no clue to any mechanism whereby the extremes of regional diversification in some species might have their origin.

In the familiar quincunxial order the proboscis hooks may be viewed as parallel

recording the number of alternating circles of hooks or the number of hooks in each longitudinal row. The number of circles is twice the number of hooks in one longitudinal row, plus or minus one, for often adjacent vertical rows differ by one hook. Among present day morphologists it is very generally the practice to express the formula of proboscis hooks in number of longitudinal rows and number of hooks in each row, indicating the observed range of variability in both counts. However, in some very primitive forms, such as the *Neoechinorhynchidae* (Figs. 4 and 5), hook designation must be by

circles because the proboscis is so short that characteristically only three circles are present. If this pattern were described in terms of longitudinal rows, alternating "longitudinal" series consist of two and one hook respectively. A similar condition wherein regimentation of the hooks conforms to circular rows only, will be discussed later. Examples will be cited from among the highly specialized Archiacanthocephala, particularly those living in mammalian hosts. In some members of this group (Fig. 18), the proboscis hooks fall readily into circles but fail to show straight longitudinal lines. The significance of this in connection with formulae used in specific descriptions will be discussed in detail. There are likewise some forms in which the proboscis hooks, at least in part, fail to conform to any exact pattern of rows.

Thus the primitive condition of small numbers of hooks (Fig. 4) and the highly specialized proboscides with distorted hook arrangement (Fig. 23), each contributes independently to a confusion of the hypothetical basic pattern of alternating longitudinal and circular rows.

Departures from a fixed hook pattern of radial symmetry fall into two distinct classes which for convenience may be grouped as teratological variations and normal variations. The latter comprise two distinguishable types, intra-specific variability in absolute numbers of hooks often evident among individuals of many species, and regional diversification which finds its chief expression in the development of asymmetry of form and size of the hooks in various regions of the same proboscis. These last named conditions provide the avenues along which evolutionary tendencies are clearly marked and often reveal evidences of specific, generic, or even greater taxonomic distinctions.

TERATOLOGICAL VARIATIONS

Orderliness in hook arrangement is so distinctive among the Acanthocephala that evidences of disorganized interruptions in the regular pattern and random scattering of supernumerary hooks stand out in bold contrast to the usual. Lühe (1912) in his analysis of variability in hook arrangement on the proboscis of *Acanthocephalus ranae* (Fig. 2) was one of the early writers to call specific attention to irregularities in pattern. He pointed to the fact that perfect quincunxial order is based on a system involving even numbers of longitudinal rows. He further showed that in *Acanthocephalus ranae* odd numbers of longitudinal rows do exist in some individuals but here some region of the proboscis suffers definite disruption of the quincunxial order. Since normal variation in number of longitudinal rows is rather great in members of the genus *Acanthocephalus*, no one has been able to determine whether this condition arises from the addition to or the subtraction from the normal even number of longitudinal rows essential to the quincunxial arrangement. No analysis has ever been able to demonstrate any regularity for the position of "seams" in proboscides possessing odd numbers of longitudinal rows.

Such anomalies suggest that the unity in plan of construction of the proboscis is not perfect, for though the pattern of the proboscis ornamentation is predetermined in the developing embryo this pattern may become disrupted by introduction of a zone of nonconformity into the usual pattern.

A second type of teratological variation is one in which the normal hook pattern becomes confused by the addition of irregularly scattered hooks not conforming to the usual rows. Such instances have been found in relative frequency (Fig. 3) among species of the genus *Centrorhynchus*.

That these are abnormal or supernumerary hooks is borne out by the fact that often they point in random direction without reference to the orientation of the normal hooks. The significance of these hooks of chaotic arrangement is not clear. They give evidence that the normal, integrated pattern is subject to individual modification that is not affected by environmental factors but must reside in the developing embryo. They thus give a basis for understanding the asymmetry of the highly specialized proboscides discussed in the following section.

NORMAL VARIATIONS

Intraspecific variability. The extent of fidelity in hook formula is far from constant in the various groups of Acanthocephala. In some of the more generalized genera, normal variability is wholly lacking and only injury or teratological variations are encountered. Such is the case in many of the representatives of the order Eoacanthocephala. Lynch (1936) examined one specimen of *Neoechinorhynchus* (Fig. 5) with the proboscis in end view and determined that there were only five hooks in each circle. Except for a few teratological instances mentioned in the literature three circles of six hooks each are so rigidly predetermined in the genus *Neoechinorhynchus* that individuals with eight (genus *Octospinifer*) or with twelve hooks to a circle (genus *Gracilisentis*) are not only specifically distinct but have other morphological features which substantiate their recognition as unquestionably valid genera. On the other hand, wide individual ranges of hook numbers are regularly encountered in many genera, especially in the two major groups Palaeacanthocephala and Archiacanthocephala. Among these plastic forms, females tend to have more rows of hooks than males of the same species and

though all direct available evidence supports the view that hook number is predetermined in the acanthella larval stage there have been some authors who have maintained that relative size of the adult worms may be correlated with number of rows of hooks independently of the sexual differences mentioned above. Thus Baylis (1927: 42) observed that in *Polyacanthorhynchus* "the number and size of the hooks also appear to increase with age of the specimen." Such conditions are extremely rare in the Acanthocephala and deserve critical restudy. Lühe (1912) in his analysis of conditions in *Acanthocephalus ranae* was one of the first to give direct attention to variability in the hook rows within a species. He found in *A. ranae* extremes of 12 and 20 longitudinal rows of proboscis hooks. The range of variability has never been tested as a possible genetic factor because of unsurmountable difficulties arising from the complicated life cycle, as well as the fact that no means of culturing these worms has ever been perfected.

Every evidence points to a genetic control of the number of hooks on the proboscis with the range of possible variability variously fixed for different species. Out of the individual variability which this control permits, in many species differentiation very commonly proceeds toward establishing groups of individuals clustered around common modes and from these groups polymorphic species give rise to new varieties and ultimately to distinct species. Often clearly defined species, differing but slightly, in other characters, are readily distinguishable on the basis of distinctly different hook formulae. Conversely, identical hook formulae may be found in distinct species readily differentiated on the basis of other morphological characters. In some instances identical proboscides on different

bodies are but the result of convergence while in other instances they seem to represent the results of speciation within an older polymorphic stock.

At one extreme, hook formulae become so rigidly fixed that only relative size of hooks supports other morphological means of differentiating species. At the other extreme, wide degree of individual variability in hook pattern provides material from which polymorphic species may become fragmented into distinct groups recognizable as either subspecies or as separate species.

Regional diversification. While perfect radial symmetry is considered as the most generalized form of hook arrangement, there are numerous factors which may disturb it. The significance of the different types of asymmetry will be discussed with particular reference to evolutionary diversifications and to application as systems for designating hook arrangement in taxonomic descriptions. For convenience of discussion these will be classed under four heads, each of which will be treated and examples cited.

1. Dorso-ventral asymmetry, specializations affecting one or more entire longitudinal rows of hooks.

2. Focal asymmetry, affecting segments of individual rows of hooks or of groups of rows.

3. Zonal asymmetry, reflected particularly in division of the proboscis into anterior and posterior zones with different hook types but also shown in the specialization of other regions of the proboscis.

4. Longitudinal condensation, whereby adjacent circles become fused.

1. Dorso-ventral asymmetry.—In cylindrical proboscides, it is not uncommon for the hooks on the ventral surface of the proboscis to be somewhat larger or at least stronger than those on the dorsal. Teleologically, this seems explainable on

the ground that with the proboscis setting at an angle to the body proper the ventral hooks serve effectively for preventing the proboscis from being pulled from its anchorage through the force of the peristaltic action of the host intestine. This teleological explanation has little merit if the operation of natural selection were offered as the means of accomplishing dorso-ventral diversification for the hooks are fully formed and perfected in the larva before becoming functional. Some inheritable factor for diversification divorced from the influence of function in the mature worms seems to be indicated in postulating any mechanism whereby dorso-ventral specialization proceeds. Orthogenesis is the avenue of evolution most directly available for diversification of the proboscis hooks when natural selection and use seem to be incapable of operation.

All degrees of dorso-ventral asymmetry are encountered, ranging from slight diversification of the two surfaces as in some species of *Rhadinorhynchus* to complete diversification as expressed in *Aspersentis* (Fig. 6) where the two surfaces are wholly unlike in form and size of the hooks and those on the dorsal show strong tendency toward disintegration of the regular plan of orientation.

Though less spectacular than conditions found in *Aspersentis*, by far the most significant instances of dorso-ventral asymmetry have come to light only recently among the members of the family Rhadinorhynchidae. Members of this family have long been choice examples of simple difference in weight and form of the hooks on dorsal and ventral surfaces of the proboscis but in *Filisoma bucerium* the hooks of the median dorsal row (Fig. 7) are specialized as blunt, horn-shaped structures though all the adjacent rows have sharp-pointed hooks.

2. Focal asymmetry.—Focal asymmetry is highly localized as well exemplified in forms such as *Arhythmorhynchus frassoni* (Fig. 8) and *Corynosoma turbidum* (Fig. 9). In these species a few enormous hooks on the ventral surface of the proboscis are wholly out of keeping with the proportions of adjacent hooks. They occupy and dominate such wide areas of the proboscis surface that the entire plan of organization of the proboscis is disturbed and rows are skewed in the regions adjacent to the enlarged hooks. In the

A parallel though different condition maintains in *Illiosentis* (Fig. 11), where a continuous circle of hooks at the base of proboscis has a few enlarged ventral hooks.

Dorso-ventral asymmetry is expressed often and in varying degrees. The hooks are laid down in early life in the invertebrate host before functional activity of grappling organs could operate to emphasize or suppress one surface over another. Nor could functional activity of surrounding parts influence the relative

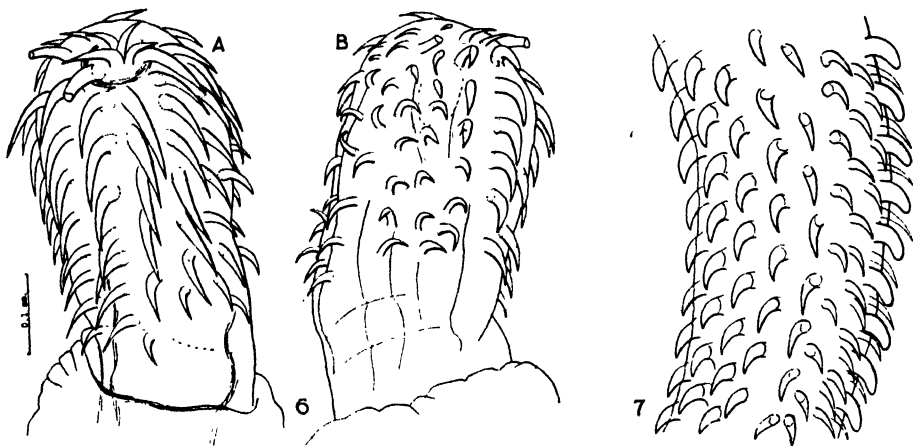


FIG. 6. PROBOSCIS OF *ASPERSENTIS* SHOWING EXTREME OF DORSO-VENTRAL DIFFERENTIATION

A. ventral surface. B. dorsal surface of the same proboscis (after Van Cleave)

FIG. 7. SEGMENT OF PROBOSCIS OF *FILISOMA BUCERIUM* SHOWING DIFFERENTIATION OF THE MEDIAN DORSAL ROW OF HEAVY, BLUNT, HORN-LIKE HOOKS (After Van Cleave)

drawing of *C. turbidum* (Fig. 9), lines connecting the hooks on the ventral surface in the region of the focal asymmetry show how spacing of rows is disturbed by the dominating presence of the enlarged hooks though actual number of hooks is not altered.

Another type of focal asymmetry is characteristic of some species of *Rhadinorhynchus*, as for instance in *R. tenuicornis* (Fig. 10), which possesses a conspicuous crescent of hooks at the base of the proboscis on the ventral surface only, not a portion of a continuous basal circle.

development of hooks. This makes it seem obvious that control of dorso-ventral asymmetry must be through the hereditary mechanism. As such it may function in sharply focused action affecting but a single row of hooks in *Filisoma bucerium*, in broader influence affecting several rows of hooks to the exclusion of others or in very broad influence marking complete dorso-ventral differentiation as in *Aspersentis*.

3. Zonal asymmetry:—Zonal asymmetry represents an extension of the disturbances characteristic of focal asym-

metry to the involvement of sectors of adjacent rows. This is most often expressed in specialization of basal portions of the proboscis and contrary to the teleological explanation offered for differentiation of the ventral hooks, zonal specialization is more often restricted to the dorsal surface of the proboscis except

clearest examples are found in *Centrorhynchus* (Fig. 12) and *Mediorhynchus* (Fig. 13) in which the anterior region is provided with hooks having prominent recurved roots while the basal region is clothed with simple, thorn-like hooks. In the two instances mentioned, the line of differentiation is fairly clearly marked

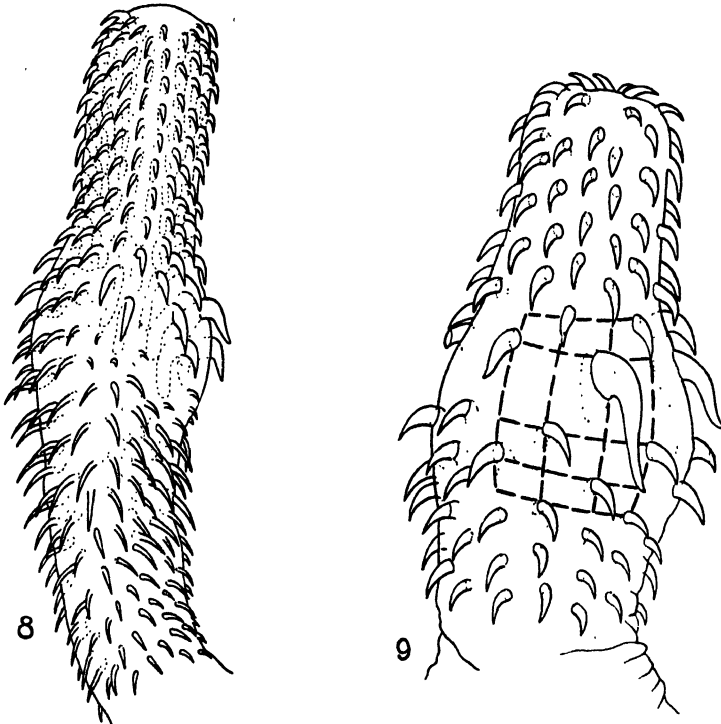


FIG. 8. *ARHYTHMORHYNCHUS FRAMONI*, PROBOSCIS SHOWING DISTINCTIVELY ENLARGED HOOKS ON THE MIDDLE OF THE VENTRAL SURFACE (After Lühe, 1911)

FIG. 9. *CORYNOSOMA TURBIDUM*, PROBOSCIS SHOWING ENLARGED VENTRAL HOOKS
Broken lines show how the symmetry in spacing of the hook rows has been disturbed (After Van Cleave)

in those instances where the entire base of the proboscis is involved.

In sharp contrast to those forms which show slight progressive diminution in size of hooks toward the proximal end of the proboscis (Fig. 1) stand those which have sharp differentiation of the proboscis into two clearly defined zones with characteristic hook types on each. The

by the line of insertion of the receptacle near the middle of the proboscis. That this morphological set-up is associated with the sharp differentiation of the hooks is further supported by the fact that in *Gigantorhynchus* the receptacle is inserted near the anterior tip of the proboscis and in this genus a single anterior crown of hooks is followed proximally by a

long series of spine-like hooks of more simple form.

One instance in which radical zonation at the base of the proboscis is divorced from the location of the line of attachment of the receptacle (Fig. 14) is in the species *Corynosoma semerme*, which has several circles of diminutive hooks posterior to the enlarged anterior region of the proboscis

ized influence have been but recently discovered. In the genus *Illiosentis* (Van Cleave and Lincicome, 1939) the four dorsal rows at the base of the proboscis (Fig. 11) show striking modifications from adjacent areas. The hooks differ in form and size from those in adjacent lateral rows and from those anterior to them in the same longitudinal rows. In



FIG. 10. *Radionorhynchus tenuicornis* ANTERIOR END OF BODY AND BASE OF THE PROBOSCIS ILLUSTRATING FOCAL ASYMMETRY IN THE DEVELOPMENT OF A VENTRAL CRESCENT OF HOOKS NOT ASSOCIATED WITH THE BASAL CIRCLE OF PROBOSCIS HOOKS (After Chandler)

FIG. 11. *Illiosentis furcatus*, BASAL REGION OF PROBOSCIS SHOWING SPECIALIZATION OF VENTRAL HOOKS IN THE BASAL CIRCLE TO FORM A CONSPICUOUS CRESCENT OF HOOKS AND THE PECULIARLY MODIFIED HEAVY HOOKS ON THE DORSAL SURFACE (After Van Cleave and Lincicome)

with its effective attachment mechanism. The small hooks here seem explainable as reduplication of the characteristic circle of small hooks which so often occurs at the base of the proboscis (see Fig. 1). Some growth or genetic factor operates toward the duplication of parts.

The most striking instances which depend upon some specific, highly local-

even more striking manner, *Tegorhynchus pectinarius* shows profound specialization (Fig. 15) in its four dorsal rows. While all the hooks at the base of the proboscis are modified as a fairly closely set comb-like structure at the base of each row, the region anterior to the comb in the four dorsal rows becomes conspicuously modified. Immediately anterior to the comb,

there is an unusually stout hook with grotesquely enlarged root. Especially in two of the rows this anomaly seriously affects the development and pattern of the hooks anterior to the large rooted hook. In some instances, the adjacent hooks are vestigial; in others, apparently lacking. This center of influence is somewhat

that region. Each papilla lying close to the line of hooks but in position between the basal and second hook imposes a slight degree of asymmetry upon the arrangement of the hooks for the basal hook becomes thrown out of line with the hooks in the same longitudinal row. The basal hook of the adjacent row is

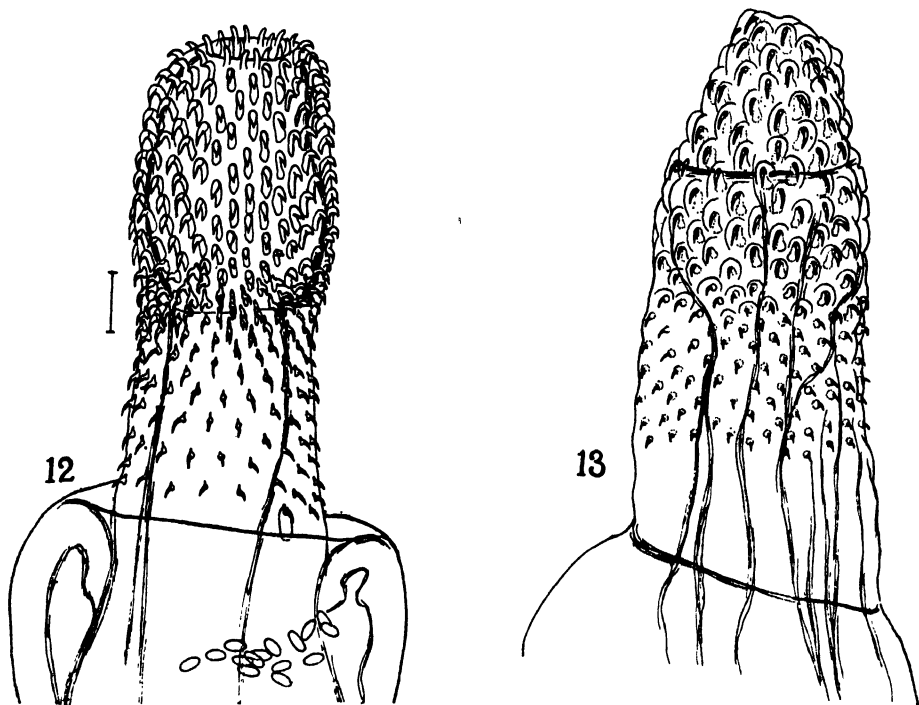


FIG. 12. PROBOSCIS OF CENTRORHYNCHUS ILLUSTRATING EXTREME DIFFERENTIATION OF HOOK TYPES OF ANTERIOR AND POSTERIOR REGIONS OF THE PROBOSCIS

FIG. 13. PROBOSCIS OF MEDIORHYNCHUS SHOWING HEAVY, ROOTED HOOKS ANTERIOR TO INSERTION OF THE RECEPTACLE AND SIMPLE THORN-LIKE HOOKS POSTERIOR TO THE INSERTION

analogous to the ventral modifications associated with enlarged hooks in *Arhytmorhynchus* and *Corynosoma* though the results are more profound in the dorsal modifications of *Illiosentis*.

In *Gorgorhynchus clavatus* the presence of a pair of small lateral papillae, which seem to be sensory in function, near the base of the proboscis disrupts the perfect arrangement of the proboscis hooks in

likewise skewed from its normal position. In fact, for two rows on either side of a papilla the hooks are disturbed in their arrangement.

4. Longitudinal condensation.—Among the conditions where quincunxial order is most clearly violated (Fig. 16) are those in species showing one or more circles with twice the normal number of hooks. Expressed in terms of longi-

tudinal rows the proboscis is described as conforming to a usual hook formula,

the proboscis there occur one or more circles of twice the usual number of hooks.

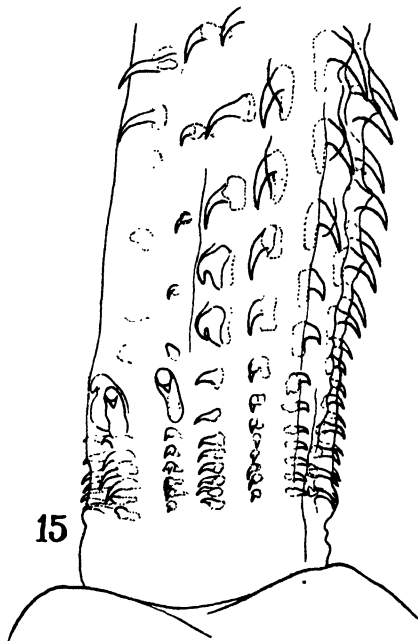
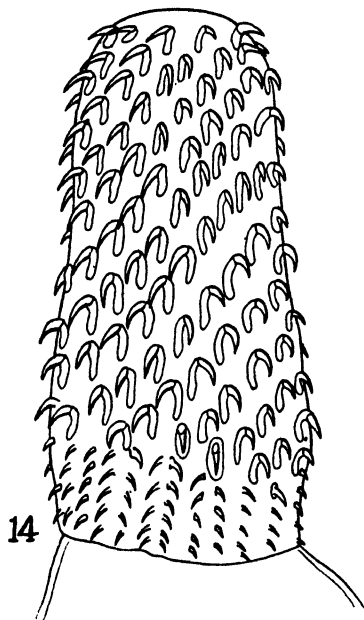


FIG. 14. *CORYNOSOMA SEMERME* PROBOSCIS, SOMEWHAT DIAGRAMMATIZED TO ILLUSTRATE THE ANTERO-POSTERIOR DIFFERENTIATION OF HOOKS IN THE SAME LONGITUDINAL ROW (After Fritschell)

FIG. 15. *TREGORHYNCHUS PECTINARIUS* BASAL REGION OF PROBOSCIS SHOWING COMPLICATED ZONAL DIFFERENTIATION, PARTICULARLY EVIDENT IN THE DORSAL ROWS (After Van Cleave, 1940)

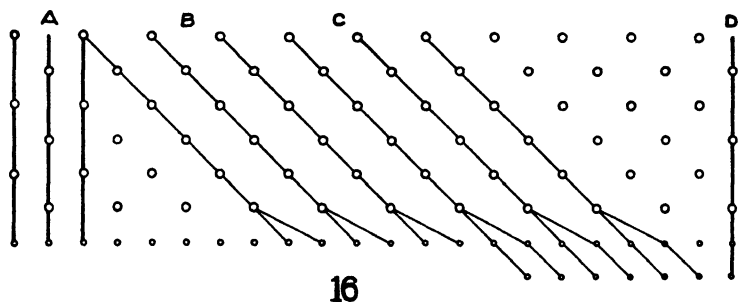


FIG. 16. ORIGINAL DIAGRAM ILLUSTRATING DIFFERENT METHODS OF DESCRIBING HOOK ARRANGEMENT

In the first three vertical lines (A) two adjacent transverse rows at the base of the series have been fused, destroying the quincunxial order, though the hooks all conform to longitudinal rows. (B) diagonal rows necessitate the introduction of bifurcation into the pattern which becomes even more evident in (C) where several adjacent transverse rows have fused. In (D) designation as a longitudinal row avoids the necessity of introducing the complicated system of bifurcating spirals.

stating the number of longitudinal rows with the number of hooks in each, then mentioning the fact that at the base of

Such instances are encountered in *Nipporhynchus* and other Gorgorhynchidae and often in the Archiacanthocephala.

In *Illiosentis* (Fig. 11) and *Tegorhynchus* (Fig. 15), adjacent rows at the base of the proboscis are so ordered that adjacent rather than alternating rows constitute cross rows or circles. This condition is obviously an extension of that found in *Nipporhynchus* in that the influence which predetermined the coalescence of two rows to form one circle has become more widely exerted until a succession of fused rows encircles the base of the proboscis giving the appearance of a new order in

However, initial fusion is the starting point of an increasing complexity which leads to complicated systems for designating hook patterns such as the one devised by Meyer. As stated above, when the hooks in *Nipporhynchus* are considered as disposed in longitudinal and circular rows, they conform readily to specification, but when the hooks are counted in diagonal, spiral rows (Fig. 16, B) those of the basal circle fail to conform with the spirals clearly evident on the remainder of

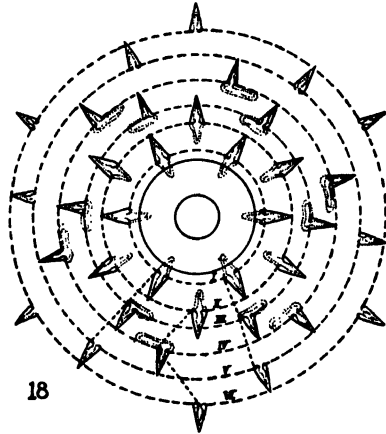
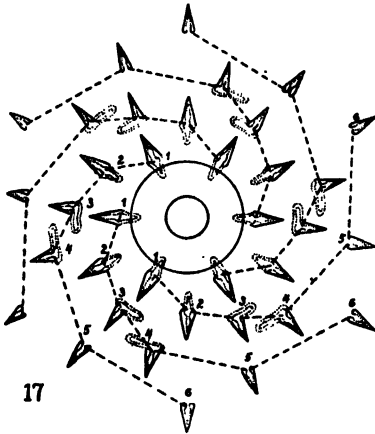


FIG. 17. THE SPIRAL ARRANGEMENT OF HOOKS IN *ONCICOLA CAMPANULATA* RECONSTRUCTED AS A POLAR PROJECTION (After Meyer)

FIG. 18. POLAR PROJECTION OF HOOK ARRANGEMENT IN *ONCICOLA CAMPANULATA* COPIED DIRECTLY FROM MEYER BUT WITH BROKEN LINES SHOWING HOW THE HOOKS FORM PERFECT CIRCLES

Alternating radial lines of hooks indicate longitudinal rows of hooks in perfect alignment but between these the radial lines are skewed.

the arrangement of the hooks. At present no avenue is available to determine if this longitudinal condensation is derived from shortening of the proboscis in the basal region or from the alternative factor of increased hook number without corresponding increase in length of the proboscis itself.

In the simplest condition, where but two adjoining circles at the base of the proboscis become fused, the relationship of the members of this basal circle to the longitudinal rows on the remainder of the proboscis is clear, as shown in Fig. 16.

the proboscis. To meet this dilemma Meyer invoked a system of branching or bifurcating spirals. The immediate comparison of the usual method of hook designation as contrasted with the system of spirals is shown in Figs. 21 and 23. When several circles at the proboscis base become fused and crowded the interpretation of arrangement becomes progressively more difficult by any manner of designation of rows, except when longitudinal condensation resulting from fusion of circles is implied.

In a relatively simple proboscis, as for

example, *Oncicola campanulata*, Meyer resorts to polar projection (Fig. 17) to explain his system of hook designation. Fig. 19 shows Meyer's interpretation of the hook order in *O. campanulata*. In Fig. 18 the same projected pattern is reduced to the more usual system of designation by longitudinal and cross rows or circles. In this instance half of the longitudinal rows are practically perfect in alignment (see Figs. 18 and 20) while in intervening longitudinal rows the arrangement

the hooks are arranged on a spheroidal surface so that meridians show as arcs, not as straight lines.

In analyzing a more complicated system of hooks, such as is found in *Pachysentis canicola*, Meyer has resorted to reconstruction in his polar projection of the pattern (Fig. 21) which is not borne out in his drawing of a side view of the proboscis of this same species (Figs. 23 and 24). In Fig. 22, Meyer's projection is copied but his lines of bifurcating spirals are

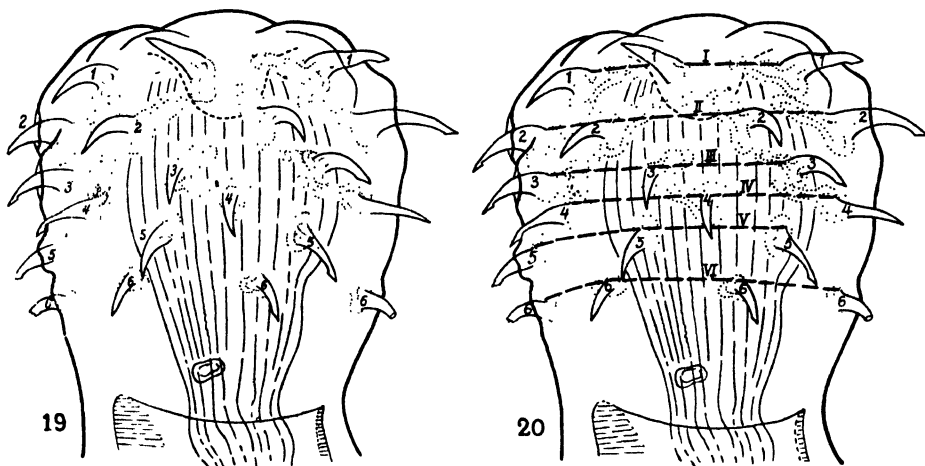


FIG. 19. LATERAL VIEW OF THE PROBOSCIS OF *ONCICOLA CAMPANULATA*, REDRAWN FROM MEYER, SHOWING WITH BROKEN LINES HOW THE HOOK PATTERN FALLS INTO PERFECT TRANSVERSE ROWS

FIG. 20. LATERAL VIEW OF PROBOSCIS OF *ONCICOLA CAMPANULATA*, REDRAWN FROM MEYER, SHOWING WITH BROKEN LINES HOW THE HOOK PATTERN FALLS INTO PERFECT TRANSVERSE ROWS

is considerably skewed from a straight line. Since polar projection is necessarily based on reconstruction, subjective interpretations are bound to enter. In Fig. 19 is presented a side view of *O. campanulata*, as drawn by Meyer and on which he based his polar reconstruction (Fig. 17). The same drawing is represented in Fig. 20 with the conventional method for designating hook arrangement. It is obvious that not all the longitudinal rows are in perfectly straight lines (see Fig. 18) but at least to some extent the skewing of the lines is attributable to the fact that

omitted and in their place it is shown that the hooks, as he has spaced them, conform to 9 circles of which the 5 apical rings and one other contain 6 hooks each, while 3 rings contain 12 hooks in each circle. This confusion is consequent upon the union of adjacent circles as mentioned for *Nippoerhynchus* earlier in this same section, except that in *Pachysentis* crowding at the base of the proboscis involves nine of the primitively twelve circles of hooks. Direct evidences of the dual nature of the fused circles is not equally clear in all of the coalesced rings. Thus

(Fig. 22) circles IV and V come near to fusion but since their component hooks show differences in size and in development of the root the two circles are readily segregated. In the reconstruction of hook arrangements shown in Fig. 22, circles VI, VII and IX represent fusion of two circles each while circle VIII stands in primitively simple form, unconfused by union with adjacent circles on the crowded part of the proboscis. However, in this interpretation Meyer is not consistent

simplicity. Accepting Meyer's Fig. 260a (which is here reproduced as Fig. 23) without any questions as to the validity of his observations, circle VII is obviously composed of hooks ordered in two levels upon the proboscis. This duplicity is even more clearly shown in the hooks of ring IX where hooks 1, 3, 5, and 7 stand anterior to the series 2, 4, and 6. Here is definite evidence that the proboscis of *Pachysentis canicola* contains primitively a pattern of seventy-two hooks ordered in

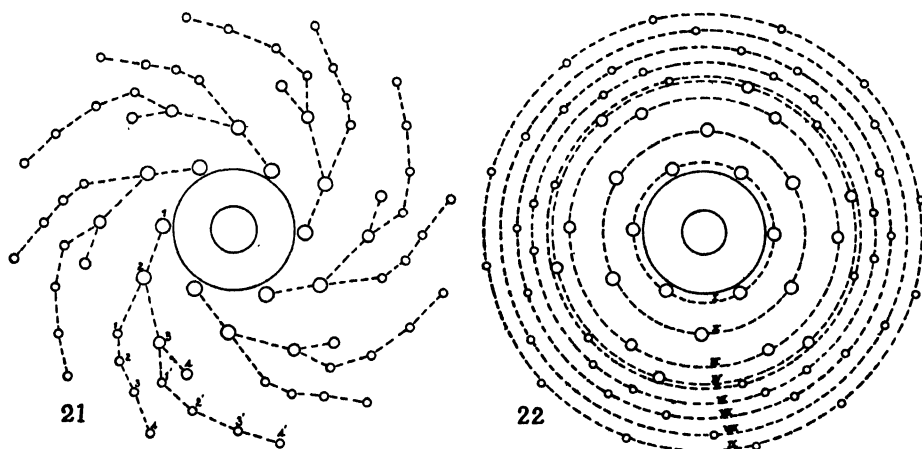


FIG. 21. POLAR PROJECTION OF HOOK ARRANGEMENT IN *PACHYSENTIS CANICOLA* SHOWING IN RECONSTRUCTION MEYER'S INTERPRETATION OF HOOKS ARRANGED AS BIFURCATING SPIRALS (After Meyer)

FIG. 22. POLAR PROJECTION OF HOOK ARRANGEMENT IN *PACHYSENTIS CANICOLA* COPIED DIRECTLY FROM MEYER, WITH CONCENTRIC CIRCLES TO REPLACE HIS BIFURCATING SPIRALS

Comparing this figure with Fig. 23, a serious error in his reconstruction is evident

with his drawing of a lateral view of the same proboscis (Fig. 23) for here cross lines have been added to Meyer's Fig. 260a to show how the hooks conform to circular arrangement before subjected to diagrammatic presentation. In this drawing of the proboscis (Fig. 23) nine circles are obvious as in the reconstructed diagram (Fig. 22) but the details regarding components of the circles do not harmonize. In Fig. 23, circles VII, VIII, and IX are coalesced rings while at the apex of the proboscis all the circles retain primitive

twelve circles of six each. By longitudinal condensation in the region of the basal portion of the proboscis six primitive circles become condensed into three. The bizarre system of bifurcating spirals invoked by Meyer rests in large measure on subjective bias in rearranging the hooks when the pattern is transposed to polar projection. Though in this instance the hooks are arranged in perfect circles they do not show alignment in consistent longitudinal rows. Since the attempt to express hook formula in either longitudi-

nal or spiral rows necessitates reconstruction and this of necessity involves subjective error it is best to refer to the hook arrangement in proboscides of this type in terms of circles only.

CONCLUSIONS

In its most generalized form, the acanthocephalan proboscis displays a relatively static specific uniformity in size and arrangement of its hooks. For example,

tudinal rows of hooks and the most available formula consists in citing the number of longitudinal rows with limits of numbers of hooks in each. In very short proboscides, the circles furnish the most characteristic basis for description of hook pattern.

The fusion of adjacent circles of hooks at the base of the proboscis offers no obstacle to expression of hook pattern in terms of either longitudinal rows or circles.

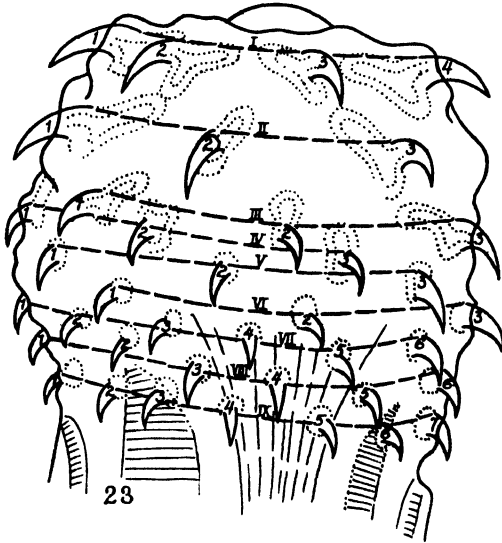


FIG. 23. *PACHYSENTIS CANICOLA*, SIDE VIEW OF PROBOSIS (After Meyer, 1932) BUT WITH BROKEN CROSS LINES ADDED TO SHOW HOW THE HOOKS FALL INTO TRANSVERSE ROWS (OR CIRCLES)

Crowding of circles at the base of the proboscis has resulted in adjacent circles becoming fused

FIG. 24. DETAIL OF HOOK ARRANGEMENT IN *P. CANICOLA* TO ILLUSTRATE MULTIPLE BIFURCATION OF SPIRAL ROWS (From Meyer)

among the Neoechinorhynchidae and many of the Echinorhynchidae form and pattern are fixed to such a degree as to suggest that a single set of relatively simple genetic factors might operate to produce characteristics having little diversification and relatively small amplitude of variability. Among these forms, which exhibit varying degrees of radial symmetry, the quincunxial pattern is most often observed. Characteristically, this pattern is most easily reduced to an expression of longi-

The introduction of an artificial system of bifurcating spiral rows of hooks as a means of describing the hook pattern fails to give recognition to the fact that crowded adjacent circles become fused, thus modifying the primitive condition of hooks arranged as perfect check rows.

Some proboscides have hooks so irregularly arranged that no system of perfect rows can be designated.

Even among the generalized forms, instances of conspicuous departure from

the normal are not uncommon, but among the more highly specialized forms of the Acanthocephala the proboscis is dynamic and highly plastic within the family and genus, though relatively consistent within the individual species. Species differ widely in the extent to which individual variability expresses itself. The proboscis shows not only wide amplitude of individual variability and incidence of abnormality but even more strikingly inherent specific tendencies toward regional specialization and development of zonal asymmetry. Both circular and longitudinal rows of hooks may singly

or in limited groups express inherent tendencies toward specialization, while within individual rows strikingly constant form differences have become established in a diversification which involves both focal and zonal asymmetry.

This dynamic concept suggests that the mechanism for hereditary control is much more highly elaborated than has been previously supposed. The form and pattern of arrangement of the hooks on the proboscis represent a mosaic, little influenced by growth or by functional relations and probably intimately predetermined in the zygote.

LITERATURE LIST

- BAYLIS, H. A. 1927. Some parasitic worms from *Arapaima gigas* (Teleostean fish) with a description of *Philometra senticosa* n. sp. (Filarioides). *Parasitol.*, 19 (1): 35-57.
- CHANDLER, A. C. 1934. A revision of the genus *Rhadinorhynchus* (Acanthocephala) with descriptions of new genera and species. *Parasitol.*, 26 (3): 352-358.
- LÜBE, M. 1911. Acanthocephalen. Die Süßwasserfauna Deutschlands, Heft 16. Jena.
- . 1912. Zur Kenntnis der Acanthocephalen. *Zool. Jahrb.*, Suppl. 15, 1 Bd.: 271-306.
- LYNCH, J. E. 1936. New species of *Neoechinorhynchus* from the western sucker, *Catostomus macrocheilus* Girard. *Trans. Amer. Micros. Soc.*, 55 (1): 21-43.
- MEYER, A. 1932-3. Acanthocephala. Bronn's Klassen u. Ordnungen des Tierreichs, Bd. 4, Abt. 2, Buch 2, Leipzig.
- VAN CLEAVE, H. J. 1919. A new genus and new species of Acanthocephala from the Antarctic. *Ann. and Mag. Nat. Hist.*, Ser. 10, vol. 1: 229-231.
- . 1936. The recognition of a new order in the Acanthocephala. *Jour. Parasitol.*, 22 (2): 202-206.
- . 1937. Acanthocephala of the genus *Corynosoma* from birds of Dyer Island, South Africa. *Göteborgs Kgl. Vetensk. Vitterb.-Samb. Handlig.*, Ser. B, 5: 1-6.
- . 1940. The Acanthocephala collected by the Allan Hancock Pacific Expedition, 1934. Allan Hancock Pacific Expeditions, 2 (15): 499-527.
- . 1940b. Relationships of the Acanthocephala. *Amer. Nat.*, 75: 31-47.
- , and D. R. LINCICOME. 1939. On a new genus and species of Rhadinorhynchidae (Acanthocephala). *Parasitol. (Cambridge)*, 31 (4): 413-416.
- , and L. H. TOWNSEND. 1936. On the assignment of *Echinorhynchus dirus* to the genus *Acanthocephalus*. *Proc. Helminthol. Soc. Washington*, 3: 63.



RESPIRATION IN THE LIVING CELL

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PREFATORY NOTE

The following review article was sent from the depths of warring China in November, 1939. I have undertaken the friendly office of preparing it for publication, but without making any essential alterations or additions. That the literature references, especially those of recent years, are incompletely reviewed, is understandable—our Chinese friends have repeatedly asked for help in the form of scientific journals. Some idea of the conditions of existence under which this review, and several experimental papers, came into being are indicated in the following quotation from a letter received from Dr. Tang at about that time. The flame of scientific adventure is not easily extinguished.

"There was established in the interior of China, Kweiyang, a medical school for the training of physicians who are to be sent to the front. I was offered to be on the scientific staff, and be responsible for the preclinical courses, and to establish labs. This I took up, and went through all kinds of hardships to get there. . . . Six months in Kweiyang to start a medical school from nothing—absolutely nothing, except a 'hospital' of four beds, and a group of determined men. But those six months were the happiest of my life. . . . The medical school has been in full swing for over a year, with four terms a year with a good staff, and now a hospital of over 100 beds, and laboratories which may well compare with any school in China in equipment. And if there is anything more satisfactory to a pioneer, the furniture, and the laboratory benches of that school are a source of joy to me, even when I am away from them. I designed everything from a three-legged stool (after the principle of the tripod, for the floors are uneven) to the actually hand-made pneumothorax machine which was rigged up from parts gotten from junk-shops all by myself, in order that a very serious case of tuberculosis may be treated. And since then, that machine, crude as it may be, has served over 200 patients.

I went to Hongkong for two months to buy equipment for the college, and in doing so, I travelled all over the southwest of China on bus, pushing the

bus most of the time, and sometimes in the dark, when no lights were available, I had two hand-torches in my hands, and ran before the bus so that we could reach the city for the night."

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A NUMBER of reviews have appeared recently on the subject of cellular respiration from the standpoint of enzyme chemistry (Meldrum, 1934; Barron, 1939; Elvehjem and Williams, 1939). We shall consider in this account the respiration of the living cell in relation to its environment. The subject under review is well defined, dealing with cells suspended in an aqueous medium, with or without added metabolite, and in an atmosphere containing oxygen; as this system responds to varying experimental conditions. The relations between the respiratory activity of the living cell and the environmental factors will when possible be expressed in formal terms lending themselves to theoretical interpretation. Only the literature relevant to this phase of cellular respiration is discussed.

INTENSITY OF RESPIRATION

The rate of respiration of a cell is changed with the state of development, the amount and kind of metabolites supplied, the nature and extent of cell surface, and the enzyme systems contained in the cell. It is obvious that, since each cell respire as a separate unit, the amount

of gas exchanged in a given time is proportional to the number of cells present; but the intensity of respiration, whether expressed in terms of number of cells or of unit weight, is of little value except for comparing like cells with respect to the variation of a particular factor, such as temperature. A few numerical values for the rates of respiration of unicellular organisms are given here to illustrate the point. Expressed in terms of cmm. of oxygen consumed per million cells per hour, *Chlorella pyrenoidosa* respire at the rate of 0.012 at 15°. This value is doubled on addition of excess glucose (Tang and French, 1933). The rate for eggs of *Arbacia punctulata*, expressed in the same units, is 33.6 at 25°, and is raised to 160 on fertilization (Tang, 1931; Tang and Gerard, 1932). The latter value is also that of *Asterias* eggs (Tang, 1931a), fertilized or unfertilized. Uniformity in rates of respiration (Q) is not improved by expressing them in terms of the gas exchanged per unit dry weight, nor per unit surface area. Although the rate of respiration for unfertilized *Arbacia* eggs is comparable with that for *Asterias* eggs, when both are expressed per unit surface, the rate of the fertilized *Arbacia* eggs is decidedly too high compared to that of the *Asterias* eggs (Tang, 1931). The table given by Specht (1934) contains further data illustrating lack of uniformity in the values of Q .

INFLUENCE OF THE KIND OF SUBSTRATE

A living cell placed in an aqueous medium without added metabolite will respire for some time at a constant rate until the foodstuff within the cell is depleted, when the rate declines. If compounds such as glucose or pyruvate are added to the solution at this time, the rate of respiration is usually greatly accelerated. However, not all organic com-

pounds are oxidized, and not all the oxidizable compounds are utilized to the same extent by the cells. There is a species specificity in the utilization of metabolites. Specificity between the organism and substrate has been tabulated for bacteria by Stephenson (1939, p. 189 *et seq.*), and Harden (1932) states that yeast will ferment glucose, fructose, mannose, and galactose. Many synthetic stereoisomers of these sugars are unfermentable, as are the corresponding pentoses, tetroses, and the alcohols.

Johnson (1936) recently made some interesting observations on the utilization of carbohydrates by two species of luminous bacteria, *Vibrio phosphorescens* and *Achromobacter Fischeri*. He showed that these species differ not only in the kind of carbohydrate utilized, but also in the rates at which the utilizable ones are oxidized. Thus, of the simple alcohols and sugars, both species oxidized only the compounds with three or six carbon atoms, and *A. Fischeri* was further limited to the reducing compounds, except for glycerol and malicose. Further, inhibition of oxidation occurred when two substances were simultaneously supplied to *A. Fischeri*. For example, α methylglucoside, though exerting no apparent influence on the oxidation of glucose, completely inhibited the oxidation of other hexoses, and retarded the oxidation of glycerol; and mannose and galactose were slightly inhibited by lyxose, the former to a greater extent than the latter. Except for the methylglucoside, mannoketoheptose was the only compound which retarded the oxidation of fructose; it also exerted the greatest retardation on mannose, galactose, and glycerol. Johnson interprets the phenomena of inhibition in terms of competition for a common adsorption surface capable of causing breakdown of the inhibited compound.

Confirming the work of Genevois (1927) and of Emerson (1927), Tang (1937) found that galactose, glucose, fructose, mannose, and maltose accelerate the rate of respiration by *Chlorella pyrenoidosa*, while lactose and sucrose do not. Of the sugars utilized, mannose is the least readily oxidized; the others accelerate the sugar-free respiration two to three times. Potassium pyruvate is readily oxidized at pH 5.4 or above, while sodium lactate at M/10 inhibits reversibly both oxygen consumption and carbon dioxide production.

The ability of a strain of yeast, *S. wanching*, to utilize different organic compounds was studied by Tang and Lin (1937). Among the substances oxidized with ease are glucose, fructose, mannose, maltose, lactose, sucrose, galactose, pyruvate, acetate, and lactate. Xylose, arabinose, and glycerol are oxidized with difficulty, if at all. Galactose, lactose, xylose, and arabinose are fermented with difficulty; while pyruvate, sucrose, maltose, mannose, fructose, and glucose are fermented with ease. Glycerol, lactate, and acetate are not utilized anaerobically, while formate, propionate, butyrate, valerate, succinate, oxalate, and citrate are neither oxidized nor fermented. The respiratory quotient is unity for yeast suspended in M/15 KH_2PO_4 with M/10 K-acetate or Na-lactate. It is 1.2 for cells suspended in M/15 KH_2PO_4 with M/10 K-pyruvate (Tang and Wu, 1938).

The value of such studies lies in the clue they may give to the nature of the enzyme systems in the cells and the relative affinities with which these enzyme systems combine with the substrates; for, other things being equal, the intensity of respiration probably increases directly with the affinity with which enzyme systems combine with the substrates. Such studies may also help to elucidate the

mode of action between enzyme systems and substrates, through absorption or competitive adsorption. And finally, the intermediate steps in the oxidation of the more complex compounds may be inferred from the feeding of simpler compounds to the cells. One method, used in the past to study the intermediate steps in carbohydrate breakdown, is to feed the cells with compounds which are presumptive intermediates. If the rate of respiration is sufficiently accelerated by the added substance, it may be an intermediate. This method has an advantage over other methods, in that the cells are maintained under physiological conditions; but the results thus obtained need confirmation by methods involving the isolation and identification of the compounds.

INFLUENCE OF SUBSTRATE CONCENTRATION

French, Kohn and Tang (1934) found that the rate of respiration of *Chlorella* cells, suspended in the dark in Knop solution without added substrate, declined with time in a manner which may be described by the equation for a first order chemical reaction until about the twentieth hour (varying according to temperature) when the rate approached a constant low level. They interpreted the results in terms of the oxidation of two different substances. This is supported by the existence of two different respiratory quotients, that of the declining phase of respiration being 1.0, while that of the constant phase is 0.65. The two phases of respiration also have different temperature characteristics.

Stier and Stannard (1936) studied a yeast, *S. Cerevisiae*, suspended in a sugar-free phosphate solution, and analyzed kinetically the rate of respiration. Confirming French, Kohn and Tang (1934) and Geiger-Huber (1934), they observed

an early declining rate of respiration, closely following the course of a first order chemical reaction, which gradually came to a constant level.

The equation for a first order chemical reaction is:

$$\frac{dx}{dt} = k(a - x) \quad (1)$$

in which a is the initial concentration of the reactant, x is the amount of the reactant transformed in t minutes, and k is a constant.

In the case of cellular respiration, the substrate concentrations x and a are usually not subject to direct measurement, and the amount of oxygen consumed is taken to be a measure of them. If we assume that the amount of oxygen consumed is proportional to substrate concentration, then a is proportional to the total oxygen consumed, A , from beginning to end of the experiment; x is proportional to y , the oxygen consumed in t ; and the rate of respiration, Q , is a first order function of $A - y$:

$$Q = f\left(\frac{dx}{dt}\right) = k'(a - x) \\ = k''(A - y). \quad (2)$$

The constant k'' is of the nature of a velocity constant, but may include other unknown terms. When a is present in excess and x is negligible compared to a , (2) may be written:

$$Q = k''A = k''' \quad (3)$$

and the order of reaction becomes zero, with a constant rate independent of substrate concentration.

When utilizable foodstuffs are added to the suspension of cells, respiration is accelerated to an extent depending on the amount of substrate. Ordinarily, an excess is added so that the rate of respira-

tion is independent of substrate concentration, but with small quantities the effect of concentration on respiration is apparent. Rubenstein (1932) added to *Sarcina lutea*, suspended in Sorensen phosphate buffers, glucose, lactate, pyruvate, and acetate, and followed respiration until the accelerating effects were over. The curve of respiration was found to follow the above equation and the apparent velocity constants were calculated. At 37°C., the constant for glucose oxidation was 0.38 in the irradiated series, and 0.41 in the dark series. At 20°, it was 0.12 in the light, 0.10 in the dark. The constants at 20° for acetate oxidation and for glucose oxidation were alike. The total oxygen consumed was only two-thirds of that required for the complete oxidation of the added metabolite.

Geiger-Huber (1934) observed, in yeast cells without added metabolite, a declining rate of respiration which came to a low and constant level after four hours. Addition of glucose accelerated the rate. Between M/10,000 and M/500, the rate of oxygen uptake was proportional to glucose concentration in the external medium, in accord with equation (2). Between M/100 and M/650, the rate was independent of glucose concentration, conforming to equation (3). Between these two limits was a range of transition. The data did not closely follow the equation of Michaelis and Menten (1913), based on a theory of substrate-enzyme complex formation. Similar experiments by Johnson (1936) on luminous bacteria, yielded data which do not lend themselves to quantitative treatment. Confirming Cook and Stephenson (1928) and Rubenstein (1932), Johnson observed that the added metabolite is only oxidized two-thirds to completion. The equation of Michaelis and Menten may be written

$$K = (E)(S)/(ES)$$

and, assuming the rate of enzyme reaction, v , is proportional to (ES) , it gives:

$$v = \frac{V(S)}{K + S} \quad (4)$$

In these equations, v is the velocity of the enzyme reaction, (S) is the concentration of substrate, (E) is the concentration of enzyme, and K is a constant. V is the maximal velocity of the enzyme reaction, obtained when E exists completely in the form of ES , the enzyme-substrate complex, the concentration of which is (ES) . $(ES) + (E)$ is kept constant throughout the course of reaction, but (S) is varied. Equation (4) is identical in form with that for the Langmuir (1932) adsorption isotherm.

Equation (4) is the expression for the velocity of a reversible bimolecular reaction with the total concentration of one reactant kept constant. The numerical value of K , the dissociation constant of the enzyme-substrate complex is given by the substrate concentration at half-maximum velocity, where $(E) = (ES)$. Assuming that the observed rate of respiration is proportional to the amount of enzyme-substrate present, Burk and Lineweaver (1934) applied the equation to N-fixing bacteria. It successfully describes the change in rate of respiration with changing substrate concentration.

We may conclude that, when the course of respiration follows a first order reaction, the concentration of substrate is probably the limiting factor, and that the apparent velocity constant is characteristic for the critical substrate being oxidized. When the equation for a rectangular hyperbola, as in (4), is followed, the interpretation may be of two kinds: either respiration is limited by the enzyme-substrate complex, the rate measures the concentration of this complex, and the constant is its dissociation constant; or rate of respiration

measures the amount of metabolite adsorbed. At present, we have no way of distinguishing between these interpretations; probably both processes are involved.

It may be noted that the constant low level of respiration of starved cells is of significance to their economy. It represents a steady state, perhaps of the transformation of an otherwise unoxidizable substance into one that is readily used. It also represents a balance between the expenditure of energy needed for maintenance of a living organism and the conservation of the available stored foodstuff.

INFLUENCE OF HYDROGEN ION CONCENTRATION

Few accounts deal with the effect of hydrogen ion concentration on cell respiration. Rubenstein (1932) found, on varying pH 1.4 to 12, that the optimum range for the respiration of *Sarcine lutea* is 5.8 to 8. More complete observations, on yeast cells, were made by Tang (1936) and Tang and Wu (1938). With phosphate buffers, there is little change in the rate of respiration between pH 5.3 and pH 7, but it falls off beyond pH 8, to zero at pH 12. In phthalate buffers, no respiration is measurable at pH 2.2 and 2.6, and is very low at pH 3. Between 3 and 3.6 there is a steep rise, and the maximum rate at 3.6 is maintained up to pH 6.2. Within the range of pH overlap, the rate of respiration of the yeast cells is alike in both buffers, and the maximum rates are equal.

In acetate buffer, however, even in an overlapping pH range, the influence of hydrogen ion concentration is markedly different. Respiration falls steeply from the maximum at 5.8 to zero at 4.2, in a logarithmic manner expressed by:

$$\frac{d \ln Q}{d \text{pH}} = K = 0.87. \quad (5)$$

This relationship between Q and pH strongly suggests hydrogen ions as the cause for the inhibition of respiration, but the failure of other buffer solutions, such as pyruvate and lactate, at the same pH range, to exert any apparent effect on yeast respiration, points to the contrary. The effect cannot be attributed to the acetate ions, since the latter are known to accelerate yeast respiration, and since no relation was found to exist between Q and the concentration of the acetate ions. Free acetic acid was thought to be the natural possible agent for the effect but, when the data were analyzed, the only relation found was an approximate linear relation between $1/Q$ and (HA) , the concentration of the free acid:

$$1/Q = k(HA) + C,$$

when Q is expressed in percentage, and (HA) in normality, k is of the order of 38,000, and $C = 0.002$. This suggests that the respiration of yeast cells is probably inhibited by free acetic acid molecules, their concentration within the cells being a function of that in the external solution (Gutstein, 1932). The inhibitory effects of 2,4-dinitrophenol (at high concentrations) on yeast (Krahl and Clowes, 1938b) and of lactates on *Chlorella* (Tang, 1937) follow a similar relation.

In borate buffer the behavior is markedly different. The rate falls from pH 6.6 to a minimum at pH 7.2, then rises again to a plateau between pH 8 and 11. This peculiar behavior in borate was traced to the formation of complex molecules between borate and glucose, which alters both the optical properties and the pH of the borate-glucose solution (Tang, 1936a). Respiration in veronal buffer does not differ significantly from that in phosphate. Oxygen consumption by yeast cells in lactate buffer is independent of pH between

3.5 and 5.5, and the rate is only half of that in phosphate with glucose at 5.8. Addition of glucose doubles the rate at the lower pH, but is less effective at the higher one. Respiration in solutions buffered with pyruvate proceeds at the same rate as in glucose-phosphate or glucose-lactate solutions, and little affected by either pH or glucose.

Evidently, the nature of the buffer used markedly influences the effect of pH on the rate of a physiological process. Different buffer anions and molecules, at the same pH range, may affect respiration differently. In the case of the phosphate and phthalate buffers, the effect of pH on respiration is very similar to the effect of pH on enzyme activity, and may be interpreted in terms of a change in the dissociation constant of the enzyme-substrate union (Haldane, 1930, p. 23). From acetate buffers free acetic acid molecules seem to penetrate the yeast cells to cause inhibition. In borate buffers, pH evidently influences the activity of glucose and its union with borate, and so the ease with which it is oxidized. Other possible effects of pH include, alteration of adsorption processes in the cell, killing of cells by hydrogen or hydroxyl ions, and change in permeability of the cell membrane to metabolites.

INFLUENCE OF TEMPERATURE

One general characteristic of all life processes is that temperature profoundly influences their rates. Within the physiological range (usually from above freezing to 40°) the relation between temperature and rate is described by certain mathematical expressions (Belehradek, 1935). The Arrhenius equation has been used extensively, especially by Crozier (1924) and his co-workers, and will be used here as an empirical tool convenient for description. Despite the incomplete

theoretical basis for application of the equation to biological processes (cf. Burton, 1936; Snyder, 1931), the temperature characteristic, μ , serves well to describe the behavior of cells towards temperature. Table 1 gives the temperature characteristics (μ) for respiration of a number of cells.

For temperatures below about 20°, the most frequently observed temperature characteristics for cell respiration are 12,000, 19,000, and 21,000, approximately.

INFLUENCE OF OXYGEN TENSION

In a normal atmosphere (air), respiration of cells proceeds undiminished when other conditions are not changed. This constant rate may be maintained even when the oxygen tension in the surrounding medium is decreased to a fraction of that in air. For this reason it has often been said that cellular respiration is independent of the oxygen tension in the surrounding medium. The effect of oxygen tension on the rate of respiration in

TABLE 1
Temperature characteristics for oxygen consumption and CO₂ production by unicellular organisms

SPECIES	TEMP. RANGE	CRITICAL TEMP.	TEMP. CHARACTERISTICS LOWER TEMP. HIGHER TEMP.			AUTHOR
<i>Chlorulla pyrenoidosa</i> (In glucose)	1°-27°	—	19,000			Crozier, Tang and French French, Kohn and Tang
(No glucose, initial phase)...	0.6°-28°	11.5°	19,500	3,500		
(No glucose, steady state). . .	0.6°-28°	—	5,600			
Yeast						
O-consumption	3°-35°	15.7°, 29°	19,530	12,440	8,290	Stier
CO ₂ -production	5°-40°	22.5°	22,200	12,250		Slator
<i>Arbacia</i> eggs						
Cytolyzed	11°-30°	—	7,200			Rubenstein and Gerard
Fertilized.	11°-30°	22°	10,800	6,500		
Resting	11°-30°	—	12,500			
<i>Azotobacter</i>	20°-30°	—	19,330			Lineweaver, Burk and Horner

The facts, that these values have been associated with hydrogen and hydroxyl ion and with iron catalysis, and that many of the temperature characteristics for enzyme activities may be associated with these values, led Crozier (1924) to suggest that μ indicates the nature of the master reaction limiting the rate of biological oxidation. Should this hypothesis be proved to be theoretically correct, an extensive study of the temperature characteristics will be very valuable.

tissues and lower organisms has been reviewed by Gerard (1931a) and by Tang (1933). When oxygen tension is much reduced, respiration varies with oxygen tension in the following manner:

$$Q = \frac{Q_0 KP}{1 + KP} \quad (6)$$

in which Q is the rate of respiration at any tension P , Q_0 is the maximum rate of respiration at the higher oxygen tensions when Q is independent of P , and K is a constant characteristic of each species of

cells and of the particular set of experimental conditions used. Tang and French (1933) studied the rate of respiration of *Chlorella* as a function of temperature and of oxygen tension and found equation (6) to apply. K changes with temperature as does the equilibrium constant of chemical reactions (that is, the Van't Hoff reaction isochore holds) according to:

$$\frac{d \ln K}{dT} = \frac{\Delta H}{RT^2} \quad (7)$$

The term ΔH is a constant, and T is in absolute units.

Assuming that the rate of respiration is limited by, and is a measure of, the amount of oxygen or metabolites adsorbed on cell surfaces, equation (6) may be identified with the adsorption isotherm of Langmuir (1932) (see Gerard, 1931a). The identical equation has been derived by Warburg and Kubowitz (1929), however, from assumed complex formation between oxygen and enzyme. The derivation follows:

Using the terminology of Warburg and Kubowitz (1929);

C_{FeO} = concentration of enzyme-oxygen complex (FeO)

C_{Fe} = concentration of respiration enzyme (Fe)

$C_{\Sigma Fe} = C_{Fe} + C_{FeO}$

$P_0 = P$ = oxygen tension in atmospheres

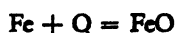
B = velocity constant for Fe oxidation

Z = velocity constant of reduction of FeO through spontaneous dissociation

Z' = velocity constant of reduction of FeO through respiration

$A = Q$ = rate of respiration.

In the reaction:



when saturated with substrate, and at stationary state,

$$\frac{-dC_{FeO}}{dt} = Bp_0C_{Fe}$$

$$-(Z + Z')C_{FeO} = 0.$$

When $Z \gg Z'$,

$$Bp_0C_{Fe} = Z'C_{FeO}. \quad (8)$$

Letting A = rate of respiration at P_0 and A_0 = maximum rate (at which $C_{Fe} = C_{\Sigma Fe}$), then at any A , the concentration of Fe as a fraction of ΣFe is given by:

$$C_{FeO} = \frac{A}{A_0} C_{\Sigma Fe}, \quad (9)$$

$$\begin{aligned} C_{Fe} &= C_{\Sigma Fe} - C_{FeO} = \left(1 - \frac{A}{A_0}\right) C_{\Sigma Fe} \\ &= C_{\Sigma Fe} - \frac{A}{A_0} C_{\Sigma Fe} \\ &= \left(1 - \frac{A}{A_0}\right) C_{\Sigma Fe}. \end{aligned} \quad (10)$$

Substituting (9) and (10) into (8), and letting $n = \frac{A}{A_0}$, and $\frac{B}{Z'} = K$, gives:

$$\frac{n}{(1-n)p_0} = \frac{B}{Z'} = K.$$

From which

$$n = \frac{P_0 K}{1 + K p_0},$$

or

$$A = \frac{A_0 K p_0}{1 + K p_0}$$

and, since $P_0 = P$, $A = Q$, and $A_0 = Q_0$

$$Q = \frac{Q_0 K P}{1 + K P}$$

which is identical with (6) above.

It is clear then that the hyperbolic relationship existing between the rate of respiration and oxygen tension does not alone distinguish between interpretations in terms of adsorption or of chemical union

of the enzyme with oxygen. Viewed as enzyme-oxygen complex formation, the constant K becomes a dissociation constant for the formation and dissociation of the complex; viewed as adsorption, K is the equilibrium constant for condensation and evaporation of oxygen from cell surfaces.

The problem of oxygen diffusion into cells as a limiting factor in respiration has been treated mathematically by Gerard (1931a). His analysis has been further generalized by Rashevsky (1938) and his colleagues in a series of papers, but only a few results (Landahl, 1937) can be given here.

Assume, for the idealized spherical cell with a coefficient of diffusion, D , a permeability to oxygen, b , and a constant rate of glucose breakdown, k : (1) that glucose breaks down to lactic acid at a rate proportional to its own concentration, (2) that lactic acid resynthesizes to glucose at a rate proportional to the square of its own concentration, and (3) that lactic acid is oxidized at a rate proportional to its own concentration and to that of oxygen. Derived equations then permit the calculation of D , b , and k .

The data of Amberson (1928), of Shoup (1929), of Tang (1931), and of Tang and Gerard (1932) were analyzed by the use of these equations, and were found to fit the theoretical curves very closely. The values of the constants for *Arbacia* eggs and for luminous bacteria are given below:

Arbacia eggs, fertilized

Data of Amberson (18°–20°)

$$D \gtrsim 3 \times 10^{-6} \text{ cm}^2/\text{min.}$$

$$b > 3 \times 10^{-2} \text{ cm/min.}$$

$$k \sim 1.5 \times 10^{-5} \text{ gm/cc/min.}$$

Data of Tang and Gerard (25°)

$$D \gtrsim 0.6 \times 10^{-6} \text{ cm}^2/\text{min.}$$

$$b > 0.8 \times 10^{-2} \text{ cm/min.}$$

$$k \sim 10^{-5} \text{ gm/cc/min.}$$

Arbacia eggs, unfertilized

Data of Tang (25°)

$$D \gtrsim 1.4 \times 10^{-6} \text{ cm}^2/\text{min.}$$

$$b > 0.7 \times 10^{-2} \text{ cm/min.}$$

$$k \sim 0.3 \times 10^{-5} \text{ gm/cc/min.}$$

Luminous bacteria

Data of Shoup (21°)

$$D \gtrsim 4 \times 10^{-6} \text{ cm}^2/\text{min.}$$

$$b > 2 \text{ cm/min.}$$

$$k \sim 2 \times 10^{-2} \text{ gm/cc/min.}$$

Although these experimental data fit the theoretical considerations very well, certain important deviations in the organisms need explanation. The constants for fertilized eggs obtained by Amberson are many times higher than those obtained by Tang and Gerard; and the temperature difference in the experiments, only about five degrees, should not significantly alter the physical constants D and b . Some physical processes have a high temperature coefficient, as the permeability to water of *Arbacia* eggs (McCutcheon and Lucké, 1932), but even so the constants should be higher for the data of Tang and Gerard, which were obtained at the higher temperature. The changes in D and in b on fertilization are of different direction or magnitude, depending on which data are used for comparison. These discrepancies are hard to explain on the basis of the analyses of Rashevsky and his coworkers.

INFLUENCE OF PHYSICAL AGENTS

The effect of hypertonic balanced solutions on echinoderm egg respiration was studied by Warburg (1930), by Loeb and Wasteneys (1913), and by Runnström (1930). The first two investigations showed that hypertonic solution increases the rate of respiration of unfertilized sea urchin eggs to the value of fertilized ones; and Runnström found the same for

hypotonic solutions. Whether hypertonic solutions increase the respiration of the fertilized eggs is still not certain. The respiration observed under these conditions is not that of intact eggs, but that of their cytolized fragments. Rubenstein (1932) studied the effect of NaCl on the respiration of *S. lutea*, from zero to five molar concentration of the salt, and found a wide optimum range between 0.1 N and about 1.8 N. Even this wide variation in osmotic pressure produced no cytolysis or other visible cell changes. Bodine (1934), studying the development of grasshopper eggs, found that hypertonic solutions caused dehydration of the cells and a drop in respiration. This was more or less reversible, depending on the length of exposure and strength of the solution with which the eggs were treated. Bodine and Boell (1936) reported that ultracentrifuging produced a marked reduction of respiration of actively developing grasshopper eggs and embryos, but not of the blocked or diapause embryos.

Irradiation of *S. lutea* with visible light increases the rate of oxygen consumption at temperatures below 30°, but decreases it at 35°, with low substrate concentration (Rubenstein, 1932). The value of the temperature characteristic for the respiration of *S. lutea* is altered by irradiation. Tang and Lin (1936) observed that the potentials at a platinum electrode placed in a suspension of *Chlorella* cells differed in light and in darkness.

Tang (1936b) found that ultraviolet light decreased the respiration of yeast, the logarithm of the percentage of respiration at any exposure being a linear function of its duration. The slope of the line is independent of temperature from 10° to 22°C. The general equation expressing the survival ratio of unicellular organisms as a function of the duration of exposure to

harmful agents such as X- and ultraviolet-radiations is:

$$N = N_0 e^{-QPt} \left(1 + QPt + \frac{Q^2 P^2 t^2}{2!} + \frac{Q^3 P^3 t^3}{3!} \dots + \frac{Q^n P^n t^n}{(n-1)!} \right), \quad (11)$$

in which N is the number of cells surviving after irradiation for a duration t (in this case, N is proportional to the amount of oxygen consumed in t); P is the probability of a quantum of radiation being effective; Q is the rate of absorption of radiant energy by the cells; e is the base of natural logarithms; and N_0 is the original number of respiring cells present (in this case, the respiration of unirradiated cells). The term n may be interpreted in two ways. If (11) is derived on the assumption that the cell is killed (and stops respiring) when a definite number of molecules is inactivated (Rahn 1934), then n represents this number. If derived on the assumption that a successive number of "quantum-hits" (Crowther, 1926; Swann and del Rosario, 1932) are necessary to kill (and stop respiration), then n represents the number of "quantum-hits." When n is unity, (11) becomes:

$$N = N_0 e^{-QPt}$$

$$\log (N/N_0) = -QPt = -\lambda t \quad (12)$$

The constant λ determined by the experiment is 0.11 at 10° or 22°, so that the Q_{10} for the process is unity.

INFLUENCE OF CHEMICAL AGENTS OTHER THAN METABOLITES

The respiration of sea urchin eggs is intensified by OH-ions, and by traces of Cu, Ag, and Au, as well as by Fe compounds (Warburg, 1930). Mast *et al.* (1936) showed that sulphur accelerated the respiration of *Chilomonas*. Heavy water was found to retard the respiration

of luminous bacteria (Harvey and Taylor, 1934) and of *Chlorella* (Craig and Trelease, 1937), though to a less extent than its photosynthesis.

The action of electrolytes on the respiration of *Chlorella* was studied by Shibata (1929) who found that cells in distilled water consumed more oxygen than did those in Knop solution and that the rate is depressed as single salts are increased in concentration. The depressing action of the salts is in the order: $K > Na > Li > Rb$, and $Sr < Mg < Ba < Ca$. The antagonistic effects are:

For Ca: $Rb < Na < K < Li$

For Ba: $Li < Rb < Na < K$

For Mg: $Rb < Li < Na < K$

For Sr: $Li < Rb < Na < K$

Pirson observed more recently (1939) that deficiency of K ions causes an increase in the respiration of *Chlorella*, and this increase is reduced as much by Rb as by K, and more by C. Green *et al.* (1939) observed a reversible inhibition of both photosynthesis and respiration when *Chlorella* is treated with copper "poisons," such as thiourea and salicylaldoxime. The concentrations required are higher than those which inhibit photosynthesis. The ascorbic acid content was found to be 0.17 mg. per ml. of centrifuged cells.

Organic dyes affect the rate of respiration of cells in a manner proportional to the redox potentials of the dyes (De Meio *et al.*, 1935); and the addition of 2,4-dinitrophenol increases the respiration of sea urchin eggs (Field *et al.*, 1934, Clowes and Krahle, 1936), yeast (Plantefol, 1933, Field *et al.*, 1934), and luminous bacteria (Shoup and Kimler, 1934). Pratt and Williams (1939) recently found that pantothenic acid, liver extract, and thiamin accelerate yeast respiration.

The respiration of yeast and *Chlorella*, among others, is inhibited by CO, KCN and H₂S, (Emerson, 1927), but such cells

as *Paramecium* and *S. lutea* (Gerard and Hyman, 1931; Gerard, 1931b; Rubenstein, 1932) are insensitive to these poisons. Narcotics such as vanillin, urethanes, diethylurea, phenylurea, propionitrile, and valeronitrile inhibit reversibly the respiration of erythrocytes (Warburg, 1928) and of *Azotobacter* (Lineweaver, 1933). Iodoacetate, although it inhibits the fermentation of yeast, has no effect on its respiration (Carol and Genvois, 1931).

Much use has been made of specific inhibitors and accelerators in the study of enzyme systems responsible for respiration, and the literature on this phase of cell respiration is very extensive. Since such studies are aimed primarily at the chemistry of the respiratory enzymes, they will not be dealt with here.

INFLUENCE OF PHYSIOLOGICAL STATE

When unfertilized sea urchin eggs are cytolyzed, either by chemical agents or by mechanical means, the fragments respire as fast as the fertilized eggs, and the bulk of respiration is carried on by the nucleated portions (Warburg, 1915). The resting rate of intact unfertilized eggs is increased following fertilization, the factor of increase depending on temperature (Warburg, 1914; Warburg and Meyerhof, 1912; Tang, 1931; Rubenstein and Gerard, 1934). This effect is not found in *Asterias* eggs (Loeb and Wasteneys, 1912; Tang, 1931a). Respiration of fucus eggs is doubled upon fertilization, that of *Neries* only slightly increased, and that of *Cummingia* and of *Chaetopterus* is even decreased (Whittaker, 1933).

A rhythmic production of CO₂ by fertilized eggs was reported by Lyon (1904) for *Arbacia punctulata*, and by Vles (1922) for *Strongylocentrotus*. Warburg (1915), Shearer (1922), and Gray (1925) failed to observe such a phenomenon in *Echinus* and *Strongylocentrotus*. The ques-

tion of a rhythmic variation in the respiration of fertilized echinoderm eggs is still not settled; for Warburg made observations at intervals too long to catch any rhythmic variations present, Gray made his runs at 10° , at which temperature respiration is too low to show any marked variation, and the data of Shearer do clearly indicate certain variations, despite his negative conclusion. When Shearer's results are plotted as rate of respiration, rather than total oxygen consumed, against time, a definite minimum is seen at the twenty-fifth minute after fertilization, when the fusion of the pronuclei occurs. The rate then gradually rises, reaching a maximum at the forty-fifth minute, and then falls to another minimum. Unfortunately, the experiment was discontinued at the sixtieth minute so that the respiration at the second cleavage was missed.

The physiological state of the cell is obviously an important factor in cellular respiration. Cells must remain intact if they are to continue to respire and their respiratory system to function properly. True, cytolyzed fragments may continue to respire, even at a higher rate than the intact cells in certain cases, but the phenomenon is only transitory, and sooner or later respiration ceases. That the nucleus is important as a locus of respiratory activity was shown by the work of Warburg, but that it is not the only center of respiratory activity is shown by the rather intense respiration of the pigmented granules in cell fragments. The recent work of Shapiro (1935), see below, also indicates that respiration is not limited to the nuclear region. The very interesting fact that the rate of respiration of different marine eggs may be accelerated, unaffected, or decreased, upon fertilization is another proof of the importance to respiration of the physiological state.

That the physical state of marine eggs is altered upon fertilization is shown by their changed permeability (cf. McCutcheon and Lucke, 1933) and viscosity (Heilbrunn, 1928), and the formation of fertilization membranes. These considerations are significant in elucidating the site of oxidations in the cell.

THE SITE OF OXIDATION

The question as to where in the cell oxidation takes place has long concerned physiologists. In a short note, Lillie (1902) reported that, when fresh alcoholic sections of frog tissue are treated with an alkaline solution of paradiamino-benzene and alpha naphthol, the nuclear region (especially the nuclear membrane) in the cells quickly turns blue, which suggests the nuclear surface is the site of oxidation. Osterhout (1917) reported that the colorless cells of the parasitic plant, *Monotropa*, turn dark by oxidation when exposed to air, and that the nuclear region is darkened most easily; again indicating that the nucleus is the site of cellular oxidation. Warburg's findings on cytolyzed cells and on nucleated and non-nucleated erythrocytes also support the hypothesis that the nucleus is responsible for the bulk of respiration in the cell. Shapiro (1935) fragmented fertilized and unfertilized *Arbacia* eggs, by high speed centrifuging, into nuclear and cytoplasmic regions and measured the respiration of the separated fragments. The unfertilized light halves, containing a nucleus but devoid of pigment, consumed oxygen at approximately the same rate as the whole cell; while the unfertilized pigmented halves, without a nucleus but possessing most of the yolk and echinochrome, displayed an oxygen-uptake 88 percent in excess of that of the whole egg. On fertilization, the light halves showed a 2.7 fold increase, similar to that shown by whole eggs, whereas the

pigmented halves did not significantly change their already high rate of respiration. These results indicate that the higher rate of respiration in the fertilized *Arbacia* eggs is primarily due to nuclear changes.

Runnström (1930) found that carbon monoxide, while barely diminishing the respiration of unfertilized sea urchin eggs, greatly increased that of the fertilized ones. Urethane actually increased resting respiration while diminishing that of fertilized eggs. On the basis of these experiments, Runnström suggested that a limited contact of respiratory enzymes with the substrate determined the reaction velocity of the resting eggs and that, consequently, considerable enzyme might be poisoned without decreasing the rate of oxidation. With these substances freed to react, by colloidal changes in active eggs, the inhibitors manifest their usual effects by combining with the enzyme. Rubenstein and Gerard, (1934) similarly interpreted their findings on the temperature coefficients of resting and fertilized eggs.

A series of experiments by Clowes and his associates (c.f. Krahle and Clowes, 1938a, 1938b), on the physiological effects of substituted phenols in relation to extra cellular and intra-cellular hydrogen ion concentration, is especially interesting and suggestive. Certain substituted phenols, notably those containing nitro- and halo-substituents in the benzene ring, reversibly block cell division and, in small concentrations, stimulate respiration, in higher concentrations, inhibit it. By using a series of such compounds, and by varying extra-cellular and intra-cellular pH, it was found that: (1) the substituted phenols penetrate the cells only in molecular form; (2) block of division is due to substituted phenol molecules in the cell; while (3) stimulation of respiration

(at low concentrations) is due to substituted phenol anions in the cytoplasmic aqueous phase; (4) inhibition of respiration (above the optimum concentration) is due to substituted phenol molecules, as is the blocking of division.

The experiments of Wertheimer (1934), although not directly concerned with oxidation, throw light on the first process in the utilization of sugar by cells. Yeast takes up sugar in accord with the adsorption isotherm of Freundlich, indicating that the first step in sugar-uptake by the cells is an adsorption process.

It may be concluded that, although the nucleus may be a locus of intensive oxidation, the entire colloidal protoplasm of the cell is responsible for the process. The fact that respiration is governed in so many ways by the colloidal properties of protoplasm leads us to believe that the oxidation is intimately connected with the colloidal state of the cell. We may perhaps picture cellular respiration as a union between oxygen and metabolites through the mediation of respiratory enzymes, the entire process taking place only when proper surfaces are provided for the anchoring and activation of the three components. In other words, cellular oxidation involves reactions in a heterogeneous chemical system composed of oxygen, metabolites, enzyme-systems, and of specific surfaces provided by the colloidal protoplasm of the cell.

CONCLUDING REMARKS

We have seen that the course of respiration in the living cell is influenced by many environmental factors, and the change of the respiratory activity with changing experimental conditions can be described by a number of formal relations. When certain assumptions are made, such as a proportionality between the respiratory rate and the amount of enzyme-

substrate present, the quantitative relations, describing the course of respiration may be identified with those describing the kinetics of enzyme and other reactions in homogeneous and heterogeneous chemical systems. Thus the course of respiration may be described by zero, first, or second order reactions; its changing rate with oxygen tension may be described in terms of the Langmuir adsorption isotherm or of the Warburg equation for enzyme-substrate complex formation; and the effect of temperature on respiratory rate may be described by Arrhenius' equation, and the change of constants with temperature by Van't Hoff's. The effect of ions on *Chlorella* respiration suggests ionic effects in colloidal systems, and the actions of poisons and of narcotics are quantitatively and specifically characteristic of chain reactions in pure chemical systems. The inhibition of respiration by ultraviolet radiation follows a logarithmic relation which may be interpreted according to the mass law in terms of the number of molecules inactivated.

As stated at the beginning, the purpose of this review is to examine the respiratory activity of the living cell from the standpoint of the kinetics of reactions in heterogeneous systems. When the relations between the rate of respiration and various experimental conditions are examined, it is found that they are adequately described by existing expressions used for the kinetics of homogeneous or for heterogeneous chemical reactions and of enzyme reactions. The theoretical implications of the identity of these formal relations must await further research, but they have at least established the generic continuity between respiration in the living cell and these physico-chemical processes.

Much of our knowledge concerning the mechanisms of chemical and enzyme reactions have come through studies on the kinetics of these reactions, and a study of the kinetics of cellular respiration may yield valuable information concerning the mechanism of the process, about which we still know very little.

LITERATURE CITED

1. AMBERSON, W. R. 1928. The influence of oxygen tension upon the respiration of unicellular organisms. *Biol. Bull.* 55: 79-91.
2. BARRON, E. S. GUZMAN. 1939. Cellular oxidation systems. *Physiol. Rev.* 19: 184-239.
3. BELSHREDAK, J. 1935. Temperature and Living Matter. Borntraeger, Berlin.
4. BODINE, JOSEPH HALL. 1934. To what extent is developmental block dependent upon the metabolic activity of the embryonic cell? *Proc. Nat. Acad. Sci.* 20: 640-644.
5. BODINE, JOSEPH HALL, and EDGAR JOHN BOELL. 1936. The effect of ultracentrifuging on the respiratory activity of developing and blocked embryonic cells (Orthoptera). *J. Cell. Comp. Physiol.* 7: 455-463.
6. BURTON, ALLAN C. 1936. The basis of the principle of the master reaction in biology. *J. Cell. Comp. Physiol.* 9: 1-14.
7. CAYROL, MM. J. et L. GENEVOIS. 1931. Inhibition spécifique de la fermentation alcoolique des cellules de levures sans arrêt ni de la respiration, ni de la réaction de Pasteur-Meyerhof, ni de la croissance. *Comptes Rendus Institut de France* 192: 1494-1496.
8. CLOWES, G. H. A., and M. E. KRAHL. 1936. Studies on cell metabolism and cell division. I. On the relation between molecular structures, chemical properties, and biological activities of the nitrophenols. *J. Gen. Physiol.* 20: 145-171.
9. COOK, R. P., and M. STEPHENSON. 1928. Bacterial oxidation by molecular oxygen. I. The aerobic oxidation of glucose and some of its fermentation products in its relation to the viability of the organisms. *Biocbem. J.* 24: 1538-1550.
10. CRAIG, FRANCIS N., and SAM F. TRELEASE. 1937. Photosynthesis of *Chlorella* in heavy water. *Amer. J. Bot.* 24: 232-242.
11. CROWTHER, J. A. 1926. The Action of X-Ray on *Colpidium colpoda*. *Proc. Roy. Soc. B.* 100: 390-404.

12. CROHER, W. J. 1924. On biological oxidations as a function of temperature. *J. Gen. Physiol.* 7: 189-216.
13. DeMEO, R. H., MILTON KIMM, and E. S. GUZMAN BARRON. 1935. Studies on biological oxidations. III. Mechanism of the catalytic effect of reversible dyes on cellular respiration. *J. Biol. Chem.* 107: 579-590.
14. ELVEHJEM, C. A., and P. W. WILSON [Editors]. 1939. *Respiratory Enzymes*. Burgess Pub. Co., Minneapolis.
15. EMERSON, ROBERT. 1927. The effect of certain respiratory inhibitors on the respiration of *Chlorella*. *J. Gen. Physiol.* 10: 469-477.
16. FIELD, J., A. W. MARTIN, and S. M. FIELD. 1934. The effect of 2,4-dinitrophenol on the oxygen consumption of yeast. *J. Cell. Comp. Physiol.* 4: 405-420.
17. FRENCH, C. S., H. I. KOHN, and P. S. TANG. 1934. Temperature characteristics for the metabolism of *Chlorella*. II. The rate of respiration of cultures of *Chlorella pyrenoidosa* as a function of time and temperature. *J. Gen. Physiol.* 18: 193-207.
18. GEIGER-HUBER, MAX. 1934. Über den Einfluss der Konzentration des Atmungsmaterials auf die Atmungsgeschwindigkeit von Pflanzen. *Jahrb. wissensch. Bot.* 81: 1-34.
19. GENEVOIS, L. 1927. Über Atmung und Gärung in grünen Pflanzen. *Biochem. Zeitschr.* 186: 461-473.
20. GERARD, R. W. 1931a. Oxygen diffusion into cells. *Biol. Bull.* 60: 245-268.
21. —. 1931b. Observations on the metabolism of *Sarcina lutea*. II. *Biol. Bull.* 60: 227-241.
22. —, and L. H. HYMAN. 1931. The cyanide insensitivity of *Paramecium*. *Amer. Jour. Physiol.*, 97: 524-525.
23. GRAY, J. 1925. The mechanism of cell division. Oxygen consumption during cleavage. *Proc. Camb. Phil. Soc. Biol. Sci.* 1: 225-236.
24. GREEN, LOWELL F., JAMES MCCARTHY, and C. C. KING. 1939. Inhibition of respiration and photosynthesis in *Chlorella pyrenoidosa* by organic compounds that inhibit copper catalysis. *J. Biol. Chem.* 128: 447-453.
25. GUTTSMAN, M. 1932. Bestimmung der H-Konzentration in der lebenden Hefe- und Bakterienzelle. *Protoplasm.* 17: 454-470.
26. HALDANE, J. B. S. 1930. *Enzymes*. Longmans, London.
27. HARDEN, ARTHUR. 1932. *Alcoholic Fermentation*. 4th. ed. Longmans. London.
28. HARVEY, E. NEWTON, and C. C. TAYLOR. 1934. The oxygen consumption of luminous bacteria in water containing deuterium oxide. *J. Cell. Comp. Physiol.* 4: 357-362.
29. HEILBRUNN, L. 1928. *Colloid Chemistry of Protoplasm*. Borntraeger, Berlin.
30. JOHNSON, FRANK H. 1936. The aerobic oxidation of carbohydrates by luminous bacteria, and the inhibition of oxidation by certain sugars. *J. Cell. Comp. Physiol.* 8: 439-463.
31. KRAHL, M. E., and G. H. A. CLOWES. 1938a. Physiological effects of nitro- and halo-substituted phenols in relation to extracellular and intracellular hydrogen ion concentration. I. Dissociation constants and theory. *J. Cell. Comp. Physiol.* 11: 1-20.
32. —, and —. 1938b. Physiological effects of nitro- and halo-substituted phenols in relation to extracellular and intracellular hydrogen ion concentration. II. Experiments with *Arbacia* eggs. *J. Cell. Comp. Physiol.* 11: 21-39.
33. LANDAUER, HERBERT D. 1937. Mathematical biophysics of cell respiration. *Growth*, 1: 263-277.
34. LANGMUIR, IRVIN. 1932. Vapor pressure, evaporation, condensation, and adsorption. *J. Amer. Chem. Soc.* 54: 2798-2832.
35. LILLIE, R. S. 1902. The role of the cell nucleus in oxydation and synthesis. *Amer. J. Physiol.* 6: xv-xvi.
36. LINEWEAVER, HANS. 1933. Characteristics of oxidation by *Azotobacter*. *J. Biol. Chem.* 99: 575-593.
37. LINEWEAVER, HANS, and DEAN BURK. 1934. The determination of enzyme dissociation constants. *J. Amer. Chem. Soc.* 56: 658-666.
38. LOEB, J., and H. WASTENEYS. 1912. Die Oxydationsvorgänge im befruchteten und unbefruchteten Seesternei. *Arch. Entwick. Organ.* 35: 555-557.
39. —, and —. 1913. The influence of hypertonic solutions upon the rate of oxidation in fertilized and unfertilized eggs. *J. Biol. Chem.* 14: 469.
40. LYON, E. P. 1904. Rhythm of CO₂ production during cleavage. *Sci.* 19: 350-353.
41. MCCUTCHEON, MORTON, and BALDWIN LUCKÉ. 1933. The effect of temperature on permeability to water of resting and of activated cells. *J. Cell. Comp. Physiol.* 2: 11-26.
42. MAST, S. O., D. M. PACER, and LOUISE MART. 1936. The effect of sulfur on the rate of respiration and on the respiratory quotient in *Chilomonas paramecium*. *J. Cell. Comp. Physiol.* 8: 125-139.
43. MELDRUM, NORMAN, U. 1934. *Cellular Respiration*. Methuen, London.

44. MICHAELIS, L., and M. L. MENTEN. 1913. Die Kinetik der Invertinwirkung. *Biochem. Zeitschr.* 49: 333-369.
45. OSTERBOUT, W. J. V. 1917. The role of the nucleus in oxidation. *Sci.* 46: 367-369.
46. PIRSON, ANDRÉ. 1939. Über die Wirkung von Alkalionen auf Wachstum und Stoffwechsel von *Chlorella*. *Planta*. 29: 231-261.
47. PLANTÉPOL, L. 1933. L'action du dinitrophenol 1.2.4 sur la respiration de levures. *Compt. Rend. Soc. de Biol.*, 113: 147-150.
48. PRATT, ERNST, and ROGER WILLIAMS. 1939. The effect of pantothenic acid on respiratory activity. *J. Gen. Physiol.* 22: 637-647.
49. RAHN, OTTO. 1934. Chemistry of death. *Cold Spring Harbor Symp. Biol.* 2: 70-77.
50. RAHEVSKY, NICOLAS. 1938. Mathematical Biophysics. Univ. Chicago Press.
51. RUBENSTEIN, B. B. 1932. The kinetics of intracellular carbohydrate oxidation of *Sarcina lutea*. *J. Cell. Comp. Physiol.* 2: 27-40.
52. RUBENSTEIN, B. B., and R. W. GERARD. 1934. Fertilization and temperature coefficients of oxygen consumption in eggs of *Arbacia punctulata*. *J. Gen. Physiol.* 17: 677-685.
53. RUNNSTRÖM, J. 1930. Atmungsmechanismus und Entwicklungsregung bei dem Seeigellei. *Protoplasma* 10: 106-170.
54. SHAPIRO, HERBERT. 1935. The respiration of fragments obtained by centrifuging the egg of the sea urchin, *Arbacia punctulata*. *J. Cell. Comp. Physiol.* 6: 101-116.
55. SHEARER, C. 1922. On the oxidation processes of Echinoderm eggs during fertilization. *Proc. Roy. Soc. Lond. B* 93: 213-229.
56. SHIBATA, M. 1929. Über die Wirkung der Elektrolyten auf den Sauerstoffverbrauch von *Chlorella ellipsoidea*. *Sci. Rep. Tohoku Imp. Univ.* 4: 431-471.
57. SHOUP, CHARLES S. 1929. The respiration of luminous bacteria and the effect of oxygen tension upon oxygen consumption. *J. Gen. Physiol.* 13: 27-45.
58. SHOUP, CHARLES S., and ALEXANDER KIMLER. 1934. The sensitivity of the respiration of luminous bacteria for 2,4-dinitrophenol. *J. Cell. Comp. Physiol.* 5: 269-276.
59. SNYDER, CHARLES D. 1931. Quantitative relations in biological processes and the radiation hypothesis of chemical activation. *QUART. REV. BIOL.* 6: 281-305.
60. SPECHT, HEINZ. 1934. Aerobic respiration in *Spirostemon ambiguum* and the production of ammonia. *J. Cell. Comp. Physiol.* 5: 319-333.
61. STEPHENSON, MARJORY. 1939. Bacterial Metabolism. 2nd. ed. Longmans, London.
62. STIRR, T. J. B., and J. N. STANNARD. 1936. A kinetic analysis of the endogenous respiration of baker's yeast. *J. Gen. Physiol.* 19: 461-477.
63. SWANN, W. F. G., and C. DEL ROSARIO. 1932. The effect of certain monochromatic ultra-violet radiation on *Euglena* cells. *J. Franklin Institute*, 213: 549-560.
64. TANG, PEI-SUNG. 1931. The oxygen-tension-oxygen consumption curve of unfertilized *Arbacia* eggs. *Biol. Bull.* 60: 242-244.
65. —. 1931a. The rate of oxygen consumption of *Asterias* eggs before and after fertilization. *Biol. Bull.* 61: 468-471.
66. TANG, PEI-SUNG. 1933. On the rate of oxygen consumption by tissues and lower organisms as a function of oxygen tension. *QUART. REV. BIOL.* 8: 260-274.
67. TANG, P. S. 1936. Studies on the kinetics of cell respiration. I. The rate of oxygen consumption by *Saccharomyces wanching* as a function of pH. *J. Cell. Comp. Physiol.* 7: 475-493.
68. —. 1936a. Studies on the kinetics of cell respiration. II. Parallelism between the rate of oxygen consumption by *Saccharomyces wanching* and the change in optical rotation of glucose in boric acid buffers. *J. Cell. Comp. Physiol.* 8: 109-115.
69. —. 1936b. Studies on the kinetics of cell respiration. III. The effect of ultraviolet light on the rate of oxygen consumption by *Saccharomyces wanching*. *J. Cell. Comp. Physiol.* 8: 117-123.
70. —. 1937. Studies on the kinetics of cell respiration. VI. Respiration of *Chlorella pyrenoidosa* in presence of lactates. *J. Cell. Comp. Physiol.* 10: 499-511.
71. —, and C. S. FRENCH. 1933. The rate of oxygen consumption by *Chlorella pyrenoidosa* as a function of temperature and of oxygen tension. *Chinese J. Physiol.* 7: 353-378.
72. —, and R. W. GERARD. 1932. The oxygen tension-oxygen consumption curve of fertilized *Arbacia* eggs. *J. Cell. Comp. Physiol.* 1: 503-513.
73. —, and C. Y. LIN. 1936. Studies on the kinetics of cell respiration. IV. Oxidation reduction potentials of *Chlorella* suspensions in light and in darkness. *J. Cell. Comp. Physiol.* 9: 149-163.
74. —, and —. 1937. Studies on the kinetics of cell respiration. V. Effect of certain organic compounds on the rate of oxygen consumption and CO₂ production by *Saccharo-*

- myces wanching*. *J. Cell. Comp. Physiol.* 10: 487-498.
75. TANG, P. S. and MAO-I WU. 1938. Studies on the kinetics of cell respiration. VII. Respiration of *Saccharomyces wanching* in acetate, lactate and pyruvate buffer solutions. *J. Cell. Comp. Physiol.* 11: 495-502.
76. VILÁ, FRÉD. 1922. Sur les variations des ions H au voisinage des oeufs en division. *Compt. Rend. Acad. Sci. Paris.* 175: 643-646.
77. WARBURG, O. 1924. Zellstruktur und Oxydationsgeschwindigkeit nach Versuchen am Seeigellei. *Pflüger's Arch. Gesamte Physiol.* 158: 189-208.
78. —. 1915. Notizen zur Entwicklungsphysiologie des Seeigelleis. *Arch. Gesamte Physiol.* 160: 324-332.
79. —. 1928. Über die katalytische Wirkungen der lebendigen Substanz. *Berlin*.
80. —. 1930. Metabolism of Tumors. [Translated by Frank Dickens] Constable. *London*.
81. —, und F. KUBOWITZ. 1929. Atmung bei der kleinen Sauerstoffdrucken. *Biochem. Zeitschr.* 214: 5-18.
82. —, und O. MEYERHOFF. 1912. Über Atmung in abgetöteten Zellen und in Zellfragmenten. *Pflüger's Arch. Gesamte Physiol.* 148: 295-311.
83. WERTHEIMER, ERNST. 1934. Über die ersten Anfänge der Zuckerassimilation. Versuche an Hefezellen. *Protoplasma* 21: 522-560.
84. WHITTAKER, D. M. 1933. On the rate of oxygen consumption by fertilized and unfertilized eggs. V. Comparisons and interpretation. *J. Gen. Physiol.* 16: 497-528.





FORM AND FUNCTION IN THE SLOTH (*Concluded*)

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Young sloths

YOUNG sloths are active almost from the moment they are born. Shortly thereafter, on emerging from the epitrichium, they crawl upon their mother and begin nursing; or they may "lose" their mother for a while and climb around in the neighboring branches or on the sides of the cage. Apparently they see well at this time. For three or four months after birth they are attractive, furry creatures; when picked up they readily crawl to the inside of one's coat, possibly for warmth, and hold on with great tenacity by their sharp claws.

While two-toed sloths guard their young jealously (Fig. 4, 3, 4), three-toed animals often show only slight regard for their offspring. Sometimes *Bradypus* may reach out and draw its young toward it, but at other times a stray baby may squeal for hours only a few feet from its mother, without any move being made by the latter to recover it. Although it clings to the sheltering breast or back with all its might, and may be dislodged only with difficulty, the young *Bradypus* may be taken from its mother with little maternal resistance. Sometimes, however, the mother may crawl away or make an attempt to fight. Males show no regard for the young.

Evidently one sloth only is born at a time; the uterus has never been found to contain more than one fetus, and mothers

have never been observed with more than one young accompanying them. The young sloth often stays with its mother for six months or more, and gradually becomes accustomed to leaving the parental fur until it finally takes its place in the jungle as a solitary wandering individual. It does not really set forth in many cases, it would seem, until the appearance of another member of the family is almost at hand. One author (Beebe, 1926) has stated, however, that the young *Bradypus* may be weaned at 4 or 5 weeks of age.

A lowly but specialized mammal

Several low-grade Eutherian characteristics are shown by sloths. Anatomically, the variable number of cervical vertebrae and the occasional presence of a complete coracoid may be mentioned. Further, the sloth skull is coarse and variable in structure, and the mandibular angle also varies in different specimens. Because of such conditions, a number of different species have been erroneously described by earlier workers. The vascular bundles, intra-abdominal testes, simple uterus and non-lobate lungs also indicate a low type of organization.

On the functional side, sloths show a low and widely-varying body temperature, and an inability to withstand moderate extremes of climate. *Bradypus* is in the latter respect greatly handicapped, and both genera are restricted to well-defined latitudes. The slow and often

irregular movements of sloths are again indicative of low-grade neuro-muscular organization and co-ordination. In keeping is the slow rate of digestion of food-stuffs. Other characteristics will be mentioned later.

Notwithstanding these and many other restrictions, the sloth appears to be the most highly adapted and specialized form for sustaining an arboreal life. Safety has of necessity been a prime factor in its evolutionary history, and marvellous clinging ability along with slow and sure movement have been developed. Life for it on land would be quite insupportable. The long, recurved claws, incapable of individual action (the manus being reduced to a hook—Fig. 14); the long, slender limbs with rotating radius and manus and pes normally facing inwards; the triangular, climbing type of scapula with large or separate coracoid, and the small pelvis—all are particular arboreal adaptations. The well-developed lateral abdominal wall and the peculiar blood-vascular plexuses may also be included.

Of the two genera, *Cholepus* is the better fitted for its habitat, and shows the greater specialization. The didactylate fore-limb and shorter hind-limb, large palmar and plantar pads (bare to aid in clinging), and complete absence of tail are striking characteristics. *Cholepus* rarely sets foot on terra firma, but *Bradypus* does fairly often. The fore-claws of *Bradypus* are somewhat longer, and those of the hind limb are shorter, than those of *Cholepus*. In *Bradypus* the fore-claws are as long as a man's fingers, and deeply grooved on the concave aspect. Comparing animals of similar weight (about 3.5 kgs.), the claws averaged in length as follows:—

Bradypus griseus:

Fore-claws, 7.0 to 8.0 cms.

Hind-claws, 5.0 to 5.5 cms.

Cholepus hoffmanni:

Fore-claws, 5.5 to 6.5 cms.

Hind-claws, 5.0 to 6.5 cms.

Bradypus is said to have lost the first and fifth toes, and *Cholepus* the fourth also in the fore-limbs. However, in a polydactylic case in which all five claws were present in the right hind limb of *Bradypus* (Fig. 14), the first digit was non-functional and the second showed only slight tonus and resistance. This would suggest the loss of the first and second toes in the normal tridactyl form.

The paws and claws may be used together very capably in drawing down and holding suspended fruits. Bananas and other fruits and objects may be held and manipulated with a nicety, indeed, when occasion demands it. It may be observed that when placed on the ground the sloth is able to oppose the manus and foot, as other plantigrade forms.

Osteology

The skull of *Bradypus* is small and ovate, and that of *Cholepus* slightly larger and somewhat more rounded. In both cases the skull plates are quite thick and strong. It is said nevertheless that the Jivaro Indians of the Amazon, known for their unpleasant custom of making shrunken mummies of their enemies' heads, employ the sloth as a subject of experiment for training boys in this art (Tevis, 1925). Wide variation in skull shape is found in different sloths. The zygomatic arch is incomplete, and the premaxillae almost absent.

The teeth are reduced to five in the upper and four in the lower jaw, incisors and canines being absent. It is interesting to note in this connection that the organs of Ackerknecht, paired epithelial bodies found under the tongue in the embryos of many higher mammalian forms and said to be related to the develop-

ment of the incisor teeth, are present in both didactyl and tridactyl sloth fetuses in which no evidence of incisors appears (Coebergh, 1930). The first lateral teeth in *Cholepus* are large, long, and pointed like canines, and the upper shear with the lower, giving great aid in feeding and constituting formidable weapons. All the teeth grow from persistent pulps and have no enamel, but a thin, hard coat of dentine is present. This forms a ridge around the upper tooth surface as the soft vasodentine enclosed wears away. No

very slowly to light. The bright yellow reflection from the tapetum of the eye at night, when a light is thrown upon it, also indicates that sloths are nocturnal in their habits.

The remarkable number of nine or even ten cervical vertebrae occurs in *Bradypus*, in contrast to the normal seven in most mammals. Cervical ribs are found on the ninth and sometimes even the eighth cervical vertebrae in this animal. There are fourteen to seventeen thoracic vertebrae. In *Cholepus* there are



FIG. 14. AN UNUSUAL CASE OF POLYDACTYLISM IN THE HIND LIMB OF THE THREE-TOED SLOTH
On the right side, five claws are present instead of the normal three

milk teeth are known. The dental characteristics thus appear to represent a primitive condition, and possibly are degenerate from a higher Eutherian type. Practically all the exposed tooth surfaces are covered with dark brown or black deposits, probably derived from the peculiar leaf (cecropia?) and fruit diet of sloths.

The eyes may be retracted deeply within the orbit at will, in both genera. Rods only are present in the retina (Wislocki, 1928), indicating that sloths are more active by night than by day. In the day the pupil is of pin-point dimensions, while at night it is wide open and responds

six (sometimes seven) cervical vertebrae, and twenty-three or twenty-four thoracic vertebrae. Miller (1935), Straus (1937), and others have discussed several aspects of the sloth vertebral column.

Considering the anatomical features of the trunk, an interesting comment has been made by Howell (1930). The construction of the chest between the pendant arms would lead one to expect a narrowing in this region, he remarks, but on the contrary the sloth chest is much broader than it is thick. Muscle pull does not appear to be an important factor therefore in the expected direction; rather, a sig-

nificant influence on the thorax has been the removal of the ventral gravitational pull, permitting the ribs to spring outward.

Skeletal muscle

While probably all other mammals possess some amount of white or pale skeletal muscle, that of the sloth is uniformly red in character (Wislocki, 1928). It would thus appear that all sloth muscle is fundamentally unsuitable for quick or delicate reactions, for which white muscle with its finer translucent fibers containing large amounts of glycogen is generally utilized. The glycogen percentage in sloth muscle is low in comparison with other animals, although to be sure this substance may not be specifically related to rapidity of action.

In microscopic sections the muscle fibers appear uniformly large and coarse, according to Wislocki (1928), and they are easily separable as distinct fibers. Cross-striations are present as in other mammalian muscle. The nerve supply shows no unusual difference from other types. From the arterial and venous plexuses in the upper parts of the limbs, vessels are said to go to and from the skeletal muscle tissues; in the muscle masses themselves, however, no unusual vascular arrangement is found.

The fact that only about half the percentage amount of skeletal muscle found in other mammals is present in sloths has been referred to elsewhere. The extremely long, thin limbs observed in animals shorn of hair, and the thin streamlined body (but not built for speed), also indicate the extraordinarily small amount of muscular development (Fig. 6). The thick, broad bands of muscle placed laterally in the abdominal wall (panniculus carnosus) are probably related to

the demands for support in the inverted position.

When operating on or dissecting out skeletal muscle, it may often be observed to undergo slow contractions of a tetanic nature.

Gastro-intestinal tract

The stomach of the sloth is extremely large, and when normally full (as it has almost invariably been observed to be, in some two hundred animals) it fills up the whole anterior part of the abdominal cavity. From twenty to over thirty per cent of the body weight may be represented by stomach and contents. After three to six days of fasting the stomach is found to be only slightly less full, and it would thus seem possible that the gastric food stores of the sloth might serve on demand for perhaps several weeks of fasting. X-ray pictures support the observation that gastro-intestinal movements progress slowly, in keeping with the general economy of the animal (see later).

On general inspection the full sloth stomach appears in the main as a large, well-rounded mass, almost as large as a man's head. Closer observation reveals some small folds on the inner curvature, indicating the presence of partially separated sacs; also, three smaller chambers are found connecting with the pylorus. A large, tapering and curving (crescent-shaped) appendage or cecum, 15 to 20 cms. long and about 5 cms. in diameter at the upper end, arises from the inferior and outer aspect of the main Bradypodine stomach. In *Cholepus* a similar appendix is present, but it is much smaller—usually about 3 cms. only in length. There are thus four distinct gastric chambers and an appendix, as well as other partially divided and probably functionally separate sacs, in didactyl and tridactyl sloths.

In many respects the tardigrade stomach resembles that of the sheep (Fig. 15).

Dissection showed a relatively thick-walled organ with many chambers, and coarse rugae and deep folds extending throughout the greater part of the main gastric chamber. Bars of muscle tissue crossed the upper part of this chamber, and connected with a large muscular ring delimiting a smaller deep chamber (Fig. 16). From the main part of the stomach

the fresh mucosa with water. This area undoubtedly represented the acid-secreting part of the stomach. Below the pylorus the intestine showed a diminishingly acid reaction for 60-100 cms. of its length.

The distal compartment adjoining the pylorus showed a heavy muscular wall, several mms. in thickness, with coarse mucosal lining (Fig. 16). Usually several grams of semi-dry, fibrous, and seedy materials were found in it. Other charac-

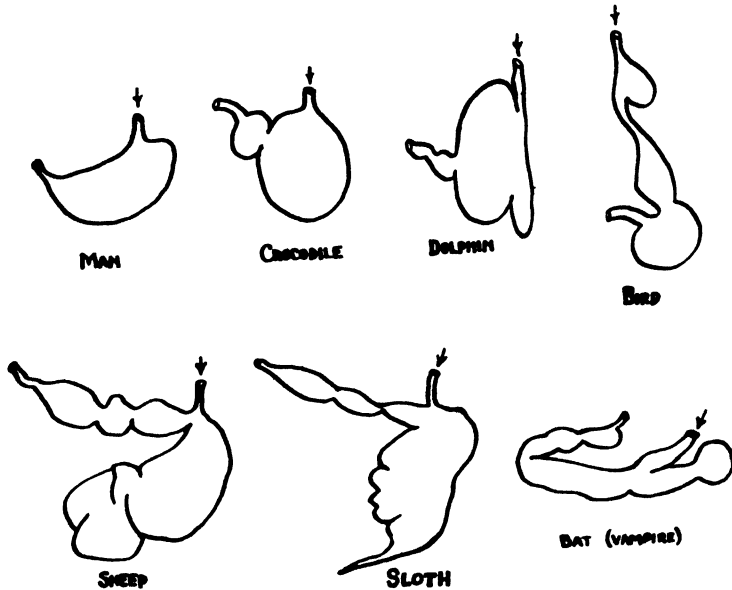


FIG. 15. A COMPARISON OF THE SLOTH STOMACH WITH THAT OF OTHER ANIMAL TYPES

the three smaller chambers, in series and somewhat cone-shaped, lead towards the intestine. The pyloric opening, not specially muscular, was about 5 cms. long by 2 cms. in diameter. The mucosa of the large gastric chamber was dull pink in color, and that of the appendix a brighter red; all other parts were a grayish color. The chambers leading to the pylorus gave acid reactions as indicated by litmus, the middle of the three showing an extremely strong reaction which did not disappear after several washings of

characteristics also present were strongly indicative of a gizzard-like organ, capable of exerting considerable pressure on contained foodstuffs. Its distinct sac formation distinguished it from an ordinary pylorus.

The gastric appendage of the tridactyl sloth is divided almost equally in half along its length internally by a strong, mucosa-covered septum; thus two orifices are present, both giving entrance to the main gastric chamber (Fig. 16). In several animals which were examined,

the appendix contained large amounts of a thick, dark green fluid, or sometimes the mass was putty-like, of uniform smooth texture and consistency. The color and character of the material suggested its similarity to bile, but this seemed hardly likely; also, several of the usual tests for this substance proved negative. No correlation of the gastric appendix with the absence of a gall bladder in this animal was apparent. In experiments in which the appendage was evacuated and then blocked by tampon at the entrances into

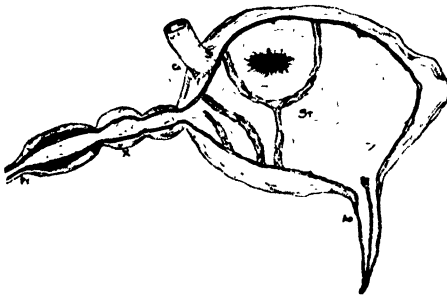


FIG. 16. SEMI-DIAGRAMMATIC SKETCH OF THE EXPOSED GASTRIC CHAMBERS OF THE THREE-TORD SLOTH

Note heavy muscle bands on the inner half of the main stomach (ST.), the long appendix (AP.) with dividing membrane, and the thick muscular wall of the pre-pyloric chamber. The chamber X gives a strongly acid reaction. CA. = cardia and PT = pylorus.

the stomach, the organ gave no evidence of important secretory activity over periods of several days, and only a small amount of mucus appeared in the cavities.

The polysacculate gastric apparatus of sloths suggests that the alimentary processes would be involved and protracted, and so indeed they are, as will be indicated later. In passing, an amusing essay by Athill (1937) contains the reflection that life for the sloth with its four stomachs "can never lack absorbing interest."

Below the stomach the intestine continues as one long, folded tube without

appendices. The transition from small to large intestine is not very marked, there being a gradual funnelling out to about twice the diameter over a length of several cms., without valvular interruption or gross change (except size) in tubal character.

A cecum is absent, as it is also in some cetacea and a few carnivores. The rectum shows a large pouch or sac in which considerable quantities of fecal masses may be stored. Anal glands are seen in *Cholepus*.

In the anesthetized sloth the exposed gastro-intestinal apparatus usually appears quiescent; cooling initiates contractions, as also does gentle manipulation. Weak faradic shocks of low frequency produce slow contractions which may extend a few centimeters along the tract. Waves of contraction may arise after exposure and partial drying of the intestines. Contractions of the lower part of the stomach appeared on electrical stimulation of the right vagus in the thorax. All the direct observations on gastro-intestinal contractions in sloths indicated that the movements were extremely slow relative to those in other forms, but otherwise similar in character.

In several didactyl sloths the gastro-intestinal movements were observed by X-rays after a barium test meal had been given. These studies (carried out on imported sloths at the University of Virginia) indicated that food such as bananas and citrus fruits may remain in the stomach from 70 to 90 hours, and even longer, after ingestion. During this time small amounts of the digested food-stuffs may be slowly passed on to the intestine, and towards the end of the period food residues begin to appear as small rounded pellets in the rectum. In some cases a week or so may be taken to make the transit of the alimentary canal!

The rectum of the experimental animal has often been found greatly distended with hard fecal pellets, a centimeter or so in diameter. The living animal may accumulate for several days and later excrete large masses of this material, up to a pound or two in weight at one time. At both ends of the gastro-intestinal tract, therefore—the stomach and rectum—the sloth shows extreme smooth-muscle sluggishness, in noteworthy agreement with its skeletal muscular slowness.

Other abdominal organs

The spleen in *Cholepus* is variable in shape and size; it is sometimes triangular and flat, but more often semi-lunar with ragged edges, about 5 cms. long by 2.5 cms. wide and 0.5 cm. thick, and 6 to 8 gms. in weight. In *Bradypus* the organ is somewhat longer and irregularly cord-like, about 7 to 8 cms. by 1.5 cms. by 0.5 cm., and 3 to 6 gms. in weight. Free accessory splenic nodules are often found.

The liver of sloths is somewhat small for the size of the animal, varying between 1 and 2 per cent only of the body weight. The smallest relative sizes are observed in the three-toed form, in which there are two main liver lobes. In the didactyl sloth there are three main liver lobes, with another lobe division only slightly marked.

deBurllet (1911), Wislocki (1928), and others have commented on an apparent rotation of the liver resulting in transposition of the lobes in sloths, and sought explanation for the condition. Broman (1929), however, states that conditions in sloths are in principle the same as in other mammals, and partial modification of mesogastria and liver ligaments has occurred because of the great enlargement of the stomach.

A small pear-shaped gall bladder, 1 to 2 cms. long, and simple with straight

neck, is found in *Cholepus* on the visceral aspect of the liver, situated centrally between the two large medial lobes and usually half buried or more in the parenchyma. The wall is of normal thickness, but appears fibrous in texture and non-muscular, and the mucosa is granular in appearance. It contains from 1 to 2 cc. of highly viscid bile. The cystic duct proceeds from the gall bladder along the inferior surface and close to the liver for a few centimeters, and is then joined by two or more (sometimes four or five) hepatic ducts which course between the lateral and central liver lobes. The common bile duct so formed then continues for about 10 cms. directly towards the small intestine, which it enters at an ampulla from 3 to 4 cms. below the pylorus (Fig. 17, A).

In the tridactyl sloth, no gall bladder is present. From the main liver lobes two larger bile ducts converge to join in the hilus, and one to three smaller ducts unite with these, without unusual enlargement, to form a common duct. The latter proceeds about 10 cms. towards the small intestine, into which it empties by a definite ampulla about 15 cms. below the pylorus (Fig. 17, B).

Attention has been drawn to the presence of a large gastric appendage in the three-toed sloth which normally contains a thick, viscid material much like bile, but gives none of the ordinary bile reactions. The possibility of a functional correlation of this organ with the absence of a gall bladder may be mentioned. By contrast, only a very small gastric appendix is found in the two-toed sloth, in which the gall bladder is present.

The pancreas is of moderate size, partly compact and partly diffuse, in both *Bradypus* and *Cholepus*. In histological preparations islets of Langerhans are observed. A duct runs through the main

mass of tissue and enters the intestine at an ampulla about 15 cms. below the pylorus in the two-toed animal, and 10 to 12 cms. below in the three-toed form.

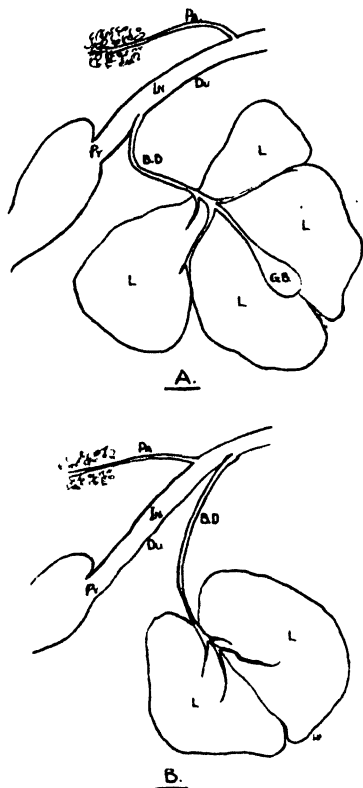


FIG. 17. SKETCH SHOWING THE RELATIONS OF LIVER (L.) AND INTESTINE (IN.), AND BILE AND PANCREATIC DUCTS (B.D. AND P.A.), IN (A.) TWO-TOED AND (B.) THREE-TOED SLOTHS

Note that in the entry of the ducts into the intestine, the relations are reversed in the two cases. There is a simple gall-bladder (G.B.) in the two-toed sloth, and none in the three-toed form. The liver in the latter animal is very small and relatively simple in type.

The relations of the bile and pancreatic ducts are shown in the accompanying illustration (Fig. 17). The entrance of the bile duct into the upper part of the duodenum well above the pancreatic duct

in the two-toed sloth which possesses a gall-bladder, and low down and distal to the pancreatic duct in the case of the three-toed animal (without gall bladder) should be emphasized. The morphological conditions possibly involve functional correlations. Obviously in the former case bile reaches the intestine and may thus act upon food materials before the pancreatic juice, while in the latter the reverse situation is present.

The kidneys and the adrenals, all relatively small organs in the adult, are in both forms of a lowly mammalian type, oval and smooth. The former are rather far down in the abdominal cavity at the rim of the pelvis, and the latter are found two or three cms. anteriorly. In several fetuses examined the adrenals were adjacent to the kidneys and strikingly large; in the smaller fetuses they were even larger than the kidneys, and consisted almost wholly of well-differentiated cortical tissue. Wislocki (1928) also observed that the fetal adrenals were in one case much larger than the kidneys. The urine in several tests was slightly alkaline in reaction, and in others slightly acid, in three-toed sloths especially.

The intra-abdominal testes are small and round and deeply situated between the rectum and bladder. Seminal vesicles have been observed in both *Cholepus* and *Bradypus*—large in the former and small and rudimentary in the latter (Wislocki, 1928). The ovary is bilobed, and is situated in a uterine pouch. The vagina is double in its lower third, and thus possesses two small outlets.

There is a small compact thymus. The thyroid is represented by a very small, rod-shaped mass on each side, with a relatively poor blood supply. Such an organ could hardly be expected to influence body metabolism to any noteworthy extent. Parathyroid glands are said to be

present (Wislocki, 1928). A description of the hypophysis has also been given by Wislocki, and special attention drawn to the absence of the pars tuberalis. The latter point emphasizes the doubt that this part of the pituitary body possesses any highly specialized function.

Respiratory apparatus

The trachea in the three-toed sloth was first described by Weber (1904), and is

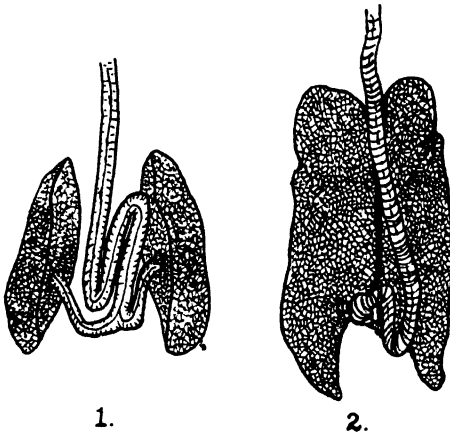


FIG. 18. SKETCH OF TRACHEA AND LUNGS IN THREE-TOED SLOTHS

1, in fetus near term, viewed anteriorly, the tracheal turns are very prominent; 2, in adult animal, seen posteriorly, the pre-bronchial ampulla is marked. The trachea in *Bradypus* is seen to be extremely long, reaching to the diaphragm and curving twice before giving off the bronchi.

strikingly unique. It is extremely long, running through the thoracic cavity dorsally and between the lungs for 12 to 15 cms. to reach the diaphragm; on the latter it recurves, proceeds anteriorly for 2 to 4 cms. and again curves slightly ventrally for a centimeter or so before opening into a sac or an ampulla about 0.75 cm. in diameter. From the latter the right and left bronchi are given off; each bronchus is 2 to 3 cms. long, of large calibre, and shows two or three

shallow sacculations. In the fetus the tracheal double turn is more defined, and the ampulla is less marked (Fig. 18). Blume (1928) has remarked on the fetal relationships. The length of the trachea to its bronchial division may be 20 cms. or more in the adult.

This long respiratory tube and the bronchi and upper respiratory passages constitute an extremely large dead space. Beyond this area, little if any freshly inspired air would pass in ordinary, quiet respiration. It would probably act as an air reservoir under some conditions, through which gaseous exchanges with the alveoli might take place for some time, even when breathing is suppressed. Thus an explanation would be offered, at least in part, for the ability of the sloth to survive immersion in water for prolonged (30 or 40 minute) periods, as well as to recover from other usually asphyxial conditions.

There appear to be no vocal cords in *Bradypus*, or at most only rudimentary tissues are present. The long, doubly-curving trachea, suggestive of an avian or reptilian condition, would therefore probably be associated functionally with the long-continued, bleating cry which may be emitted by this animal. In didactyl sloths the tracheal arrangements and vocal cords are similar to those found in other mammals.

There are slight indications only that the lungs may be divided into upper and lower lobes (Fig. 18, 2). The respiratory surface is apparently extremely small compared to other animals. While the number of air cells (alveoli) in the cat, for example, has been estimated at 400,000,000, and the respiratory surface is equal to about 20 square meters, the respective figures in the sloth were only 6,250,000 cells with a surface of 5 square meters (Howell, 1930).

The respiratory rate varies in different animals from 10 to 15 cycles per minute, and rises on excitement or activity to 20 to 30 per minute. Normally, a rather shallow type of breathing is observed. The usual effects of vagal nerve section and stimulation, the Hering-Breuer reflex, and CO₂ effects are observed in sloths as in other mammals (Almeida, 1928).

Tissue and organ weights

About 20 per cent of the body weight of sloths consists of skin and hair, about 25 per cent is muscle, 20 to 25 per cent bone, and 25 per cent stomach and intestines. A striking amount of the animal is therefore skin and bone, and these tissues together with the ponderous alimentary tract and contents constitute a tremendous burden for the relatively small amount of skeletal muscle in this animal. The muscle is only a little more than half the percentage amount found in most other mammals.

The heart of sloths is considerably smaller than in other mammals, being less than 0.3 per cent of the body weight. The three-toed sloth has a very small liver—a little over 1 per cent of the body weight; in the two-toed animal it is also rather small—about 2 per cent of body weight. The intra-abdominal testes in all sloths are very small—only 0.13 per cent of the body weight. The brain (including cerebellum), in several cases which were examined, was about 0.6 per cent of the body weight, a high figure for a low-type of mammal. It should be said that in these and all other cases determinations were made on day-fasting animals, and no corrections were made for the large stomach, fecal residues, etc., found in sloths.

Figures for other organs observed by the author, given in percentage of body weight, are as follows:—Two-toed sloths:

kidneys 0.54, spleen 0.19, pancreas 0.33, adrenals 0.02, ovaries 0.03, lungs 0.59. Three-toed sloths: kidneys 0.43, spleen 0.11, pancreas 0.33, adrenals 0.015 (male) and 0.022 (female), ovaries 0.03, lungs 0.79. Combined weights are considered in the case of bilaterally represented organs.

Blood and circulation

In operative procedures on sloths the tissues appear somewhat pale and do not bleed readily, and it would seem that these animals are not as vascular as most higher forms. However, blood volume levels have not been ascertained. It is rather difficult to secure a few cc. of blood, from tridactyl sloths especially, unless a rather large vessel be entered. Probably the relatively low pressures in the vascular plexuses are explanatory of the conditions. A good systolic arterial pressure between 120–140 mm. Hg is maintained in didactyl animals, and vascular responses to adrenal stimulation and various excitatory conditions are in keeping with those derived from other types.

Reference has been made to the work of Wislocki (1928) for many points on the circulation in sloths. The brachial, hypogastric, and iliac arteries are said to send off numerous small vessels to form remarkably rich arterial plexuses (retia mirabilia), running for some distance with the main arteries, in the fore and hind limbs. In close correlation is a plexiform arrangement of small veins with anastomoses returning blood from the limb areas.

The small arterial vessels are found to run in close bundles surrounded by connective tissue for some distance before branching off to the muscles; along with the venous plexuses they are chiefly noticeable in the proximal parts of the limbs. Somewhat similar conditions have been found in other Edentates and

in some marsupials, rodents and other forms; they are observed particularly, however, in the older or less differentiated mammalian types, and probably represent an archaic condition.

Much discussion has ensued regarding the function of such unusual vascular plexuses. From all appearances they serve specifically the skeletal muscle tissues, and many have suggested their possible involvement in the maintenance of blood flow during slowly-developed and long-sustained tetanic contractions. That such a manifold vascular branching would result in a very low blood pressure in the small vessels eventually reaching the muscles would appear certain. The conditions would nevertheless facilitate the *perfusion* of blood through all the muscle fibers, and serve to maintain the flow continuously under the peculiar and difficult gravitational influences involved in the "upside-down" position. The amount of blood flowing in unit time through a unit of muscle tissue, that is to say, would be well maintained. The plexiform arrangement of veins, as well as the posture of the animal, would also materially aid in venous return to the heart.

It would appear therefore that a functionally simplified blood-vascular apparatus is provided for the limbs, in inactive or posturally unique forms such as the sloth. It may be remarked further that the metabolic demands for the simple maintenance of tone—and the sloth is occupied most of its life in keeping up *tonus*—are much smaller than for actual contraction of muscle, and the supply of blood at a high pressure would not be an imperative demand.

Sloths and other Edentates usually possess a double vena cava, or two venae cavae, one on either side of the aorta, which unite mid-abdominally. In the

sacral region large branches are given off and enter the vertebral canal to unite with other veins there, and thus much of the blood from the hind limbs reaches the heart by a relatively abnormal manner via several enlarged thoracic intervertebral foramina, without going through the liver. Posture and gravity influences have possibly brought about this very unusual vascular arrangement, although somewhat similar conditions said to have been detected in ground-living "ancestors" of present-day sloths would tend to invalidate a mechanical explanation (de Burlet, 1922; Wislocki, 1928; Wislocki and Straus, 1932).

The blood cells of sloths are not notably different from those observed in most other mammalian forms. The erythrocytes may sometimes be found elliptical or distorted in smears, but for the most part they appear as circular biconcave discs. The leucocytes seem rather small compared to other types, but no special study has been made of these cells. Free histiocytes have been observed in sloth blood (Oria, 1929).

Some determinations of blood constituents have been made in the course of other studies. The blood sugar in both *Cholepus* and *Bradypus* approximates the levels found in other mammals—usually between 75 and 95 mgs. per cent, with a range of 65 to 165 mgs. In disturbances such as emotion, increases of 50 per cent or more above normal may occur fairly readily. Serum sodium, potassium and chloride levels were on the average 130, 5.5 to 7.5, and 100 mE. per liter respectively. The values for sodium and chloride are observed to be much lower—from 10 to 25 per cent—than in animals such as cats or dogs. The urea in the serum averaged 100 mgs. per cent in two-toed sloths, and 80 mgs.

in the three-toed form—in both cases much greater than in most mammals.

Sloths appear to be richly supplied with lymphatic vessels and glands, the latter being rather small in the thoracic and abdominal cavities. Wislocki (1928) has observed that in the abdominal area the lymphatics empty into the vena cava and portal vein, and no thoracic duct is therefore formed.

The heart

The heart rate in *Bradypus* in the quiet state is usually between 60 and 110 per minute, and in *Cholepus* somewhat higher, between 70 and 130 per minute. Fairly quick accelerations of 20 to 40 per cent are observed on exercise and excitement, and also on adrenal massage. Inhibition occurred almost immediately on stimulating the vagus nerve in the neck in *Bradypus*, and in the thorax just above the heart in *Cholepus*. Both right and left nerve stimulation was effective, and the heart rate was reduced to 20 or 30 beats per minute. No standstill was produced. In several attempts, vagus stimulation in the cervical region, however, was without effect in *Cholepus*. Electrocardiographic records were essentially similar to those derived from most other mammals.

The heart is moderately well supplied with glycogen, usually averaging between 0.5 and 0.6 mg. per cent.

The extremely small size of the heart in sloths—about half that found in man and high-class mammals, in relation to body weight—would in itself place definite restrictions on the movements of these animals.

Body temperature and metabolism

The variable body temperature of sloths has been noted by Kredel (1928). Wislocki (1933) also has discussed this

subject from the viewpoint of intra-abdominal testicular function.

In recent studies (Britton and Atkinson, 1938) it has been pointed out that the average rectal, gastric, muscular, and cardiac temperatures in sloths are from 3° to 6° C. lower than in most mammalian types. The three-toed form showed the lower and more variable temperature. Exposure of sloths to moderately cold air (10° to 15°C.) resulted in a rapid loss of body heat. Within four to seven hours the rectal temperature was reduced to about 20°C., and a state of cold narcosis similar to a hibernating condition set in, without the occurrence of shivering. Recovery of normal temperature occurred on exposure to a warm atmosphere. In this connection it may be observed that sloths show very little abdominal and no subcutaneous fat deposits.

Sloths that were placed in ordinary direct sunshine in the tropics (35° to 40°C.) showed a sharp rise in rectal temperature to a lethal level (40°C.) in about two hours. Panting and other evidences of hyperthermia became extreme, and several animals succumbed from such experiences.

These observations, along with other unpublished data showing wide body temperature changes with diurnal fluctuations in air temperature, indicate that sloths possess a very limited thermoregulatory mechanism. Indeed, these animals, especially the three-toed form, may be considered as poikilothermic in character, since their body temperature varies in agreement with and only a few degrees above that of their surroundings. They are probably not far removed in this and some other respects from an ancient reptilian ancestry.

In captivity in large open-air pens in the tropics, sloths almost invariably seek the deepest shade during the warmer part

of the day, or from 10 A.M. to 4 P.M. In the depths of the jungle forest the air temperature is said to vary but little from 30°C. throughout the year, and here the sloth abounds. Its long, hairy coat and thick skin are highly insulatory, and considering also its sluggish mode of life in a relatively thermostable habitat, almost ideal conditions are present for maintaining a not-too-widely fluctuating body temperature with the least expenditure of energy.

From many aspects it appears that the metabolism of the sloth is extremely low. One report (Almeida and Fialho, 1924) states that in the case of *Bradypus tri-dactylus* the basal metabolic rate showed an output of 11 to 12 Cals. per square meter of body surface per hour, in striking contrast to the normal mammalian average of approximately 40 Cals. Thus its caloric output would seem to be only 25 or 30 per cent of that shown by most higher animal types. Besides further considerations involving low body temperature and general inactivity, the small amount of skeletal muscle tissue relative to body weight possessed by the sloth also is significant. The very large, complex gastric apparatus, amazingly tardy in function, would further contribute to the lethargic scheme of life.

It may be observed in connection with the above that sweat glands, as well as sebaceous glands, are said to be absent in *Choloepus* (Walter, 1928). They are present in large numbers on the snout, however, for the animal shows beads of perspiration here, but not on the foot-pads, when experimentally overheated. Moreover, Wislocki's careful work (1928) has shown that while in *Bradypus* the sweat glands are extremely small and infrequent, in *Choloepus* they are present all over the hairy portion of the body and nose. It can hardly be imagined, how-

ever, that sloths would ever need to eliminate heat rapidly by sweating, under normal conditions. They may nevertheless move sufficiently to raise their body temperature a degree or so, after long provocation (Britton and Kline, 1939), and exposure to direct tropical sunshine for a few hours may warm up an animal above normal; but these are quite abnormal conditions. In the event of hyperthermia, panting with mouth open and tongue out occurs, and thus some excess heat may be lost.

Carbohydrate metabolism

Comment has already been made on the blood-sugar levels in sloths, which is fairly normal for mammals and averages about 85 mgs. per cent. Glycogen values in various tissues were found to average as follows: Two-toed sloth (10 cases): liver 0.50, muscle 0.42, and heart 0.48 per cent; three-toed sloth (13 cases): liver 0.54, muscle 0.47, and heart 0.61 per cent (Britton, Kline, and Silvette, 1938). These are rather low figures compared to those found in other mammals. In view of the fact that in all cases examined the animals were digesting carbohydrate materials (this was so even after several days of fasting), the liver glycogen levels appeared notably low. They were indeed less than 50 per cent of the mammalian normal. The small size of the liver in the sloth—about half that found in higher forms—may also be recalled in this connection. The conditions suggest functional limitations, although the rate of glycogen formation and liberation is an important consideration to be borne in mind. Several tests were made to determine the conditions present, with the following results.

Subcutaneous adrenalin injections in large amounts up to 1 cc. of 1:1000 solution, tested on both two-toed and three-

toed forms, resulted in only slight increases (10 or 15 per cent) in the blood-sugar level. Apparently glycogen reserves were not readily mobilizable.

Insulin administration was withstood rather poorly by both *Bradypus* and *Choloepus*, even in the non-fasting condition. Convulsions occurred in three to four hours with the smaller doses used, and none of the three-toed sloths recovered. In several instances the two-toed animals made good recovery, however, after showing profound depression for a day or so from a single dose of insulin.

Adrenalectomy resulted in death, usually within 24 hours, after marked losses (50 per cent or more) in blood sugar and liver glycogen. Important reductions were observed also in skeletal muscle and cardiac glycogen. This very rapid death after adrenal removal, correlated with severe losses in carbohydrate materials in the presence of large amounts of food in the gastro-intestinal tract, is again of considerable significance.

In all cases in which pancreatectomy was carried out, moderate hyperglycemia (200 to 300 mgs. per cent) developed, but not until three or four days had elapsed after operation. These and the foregoing results all point, therefore, to a slowly-acting, low-grade glycotoxic mechanism in the sloth.

The brain: decerebration

It has been observed that the weight of the brain in sloths appears fairly high (see above), considering the animal's low scale of life. Sketches of the dorsal surface markings are given herewith (Fig. 19).

Reaction times in the tridactyl sloth have been found to be slower than in the didactyl form (Langworthy, 1935), in keeping with observations on general daily activity, herein noted. The flexor

muscles are said to be anti-gravity in type, and extensor responses of the limbs on stimulation of cortical areas are found to be predominant. Several cortical motor areas were delimited by Langworthy, and the facial and other regions were notably more differentiated in the two-toed form.

From common observation, it is evident that responses to touch are prompt and well defined, and taste and smell are also well developed. Sight (by day) and hearing appear very limited in comparison with higher forms.

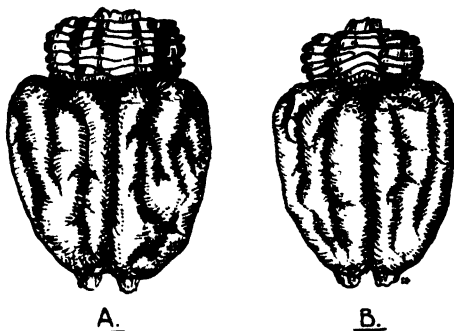


FIG. 19. THE BRAIN OF (A.) TWO-TOED AND (B.) THREE-TOED SLOTHS, SKETCHED FROM ABOVE

That of the two-toed form is somewhat more richly marked. Areas from which muscular responses have been produced on stimulation are similar to those in higher mammals.

Richter and Bartemeier (1926) have stated that decerebration in the sloth results in a flexor rigidity rather than an extensor condition as observed in other mammals. This was to be expected, these workers remarked, on the basis of the principle reached by Sherrington in his work on animals maintaining the upright posture. In our own experiments we have noted, however, the occurrence of both extensor and flexor rigidity in sloths after decerebration: in different animals the one or the other condition predominated. Also, flexion

was observed early after operation, while extension usually appeared later. These results will be discussed elsewhere (Britton and Kline, 1941).

Operative procedures

It should be emphasized that most operations on the sloth are withstood extremely well, and on many counts this animal is excellent for physiological studies. By approaching it from behind it may be taken and held fairly easily, although the limbs may have to be removed one at a time from the cage wall or a branch to which they cling most tenaciously. There are difficulties in keeping the animals alive in northerly latitudes, and experimental work should preferably be done in the natural habitat of the sloth.

After bilateral nephrectomy the sloth usually remains in good condition for a few days to a week (in one case, 176 hours), when death supervenes as in other forms with high blood urea values. Glycogen losses in skeletal muscle and liver are also marked. Thyroidectomy was non-fatal in one case observed, but activity was reduced even below the normal sloth level. Depancreatized animals survived for a week or more in good (but diabetic) condition. After extensive brain destruction or low decerebration, good responses were shown for several days.

Removal of the adrenals was the only operation studied which resulted in very rapid deterioration and death: in some cases the survivals were only 12 hours, and the average of all cases was 26 hours. The operation itself was very simple, and symptoms and deaths were typical. It is therefore clear that sloths are greatly dependent on proper adrenal function for even their very leisurely pace of living. How much more then, may we say, are

higher mammals with their comparatively terrific living tempos dependent on the normal functioning of the adrenal mechanism.

THE SLOTH'S SLUGGISHNESS

There are a number of anatomical and physiological features of the sloth which tend to make it the slowest of all living mammals. In this connection the following points may be summarized briefly from the foregoing discussion:

Sloths possess a relatively small amount of skeletal muscle tissue, all of it being of the slowly-reacting (red) type and possessing a physiologically low-grade, low-pressure blood supply.

There is a very small respiratory (pulmonary alveolar) surface, and a large dead space (three-toed animals).

A small heart, and small thyroid and adrenal glands, are present.

The liver is small in size and shows low glycogen reserves, and functional tests indicate very limited carbo-metabolic abilities.

The stomach and rectum with their contents are very ponderous, and the rate of digestion and absorption is extremely slow.

The skin is almost inelastic, and there is a heavy coat of hair.

There is a poorly-developed sense of equilibrium, and the reflexes are slow.

The body temperature and basal metabolism are relatively much lower than in other animals.

Although many other conditions are probably also involved, the above constitute a striking list of restrictions and embarrassments to an active life. It is interesting to observe that an efficient means for even further depressing sloth activity is found in the well-developed vagus nerves, which on coming into play may reduce cardiac rate (and thus affect

circulatory and general body conditions) to 10 per cent only of its normal level. On adequate stimulation the sympathico-adrenal mechanism may on the other hand bring about greatly heightened circulatory and muscular responses, which may even approximate some of those observed in the higher mammals.

On deslothing the sloth

Several ways of speeding up the sloth from its (anthropomorphically-considered) sluggishness have been noted (Britton and Kline, 1939). The rate of travel along the under side of a 12-foot horizontal pole, timed by stopwatch, was used as a test. To this the sloth became readily accustomed.

Raising the temperature of the animal appeared to be the best stimulator. Mere exposure to the tropical sun for a short while, resulting in elevation of the body temperature a few degrees, augmented activity on the average 50 per cent, and in some cases over 100 per cent. Again, setting up an emotional reaction in the sloth, by simple feints and passes before it, increased its speed markedly. The administration of various substances, such as adrenalin, prostigmin and cortico-adrenal extract, also provided an adequate stimulus to increased activity. Cortico-adrenal extract appeared to maintain the increased rate of upside-down travel by the sloth for 10 or 12 hours after injection, in keeping with earlier observations on the dog (Eagle, Britton and Kline, 1932). Prostigmin as well as emotional stimulation brought out the fighting instinct, along with the greater ability to "run" away.

The rate of progress of the sloth may be determined approximately from our data on a mileage basis. It appeared from several hundred tests (Britton and Kline,

1939) that the two-toed sloth normally averaged a little over three hours to the mile, and three-toed animals almost four-and-a-half hours. The slowest individual tardigrades, however, took over six hours for the distance. Under excitation such as that noted above, the mile was possible in about two hours, and in a burst of speed by one animal only, a mile an hour was accomplished. In a few comparative tests, turtles and tortoises were observed to travel at about the same rate as sloths.

When placed on a smooth plane surface the sloth is unable to move forward, but in the grass or on earth it pulls itself along by dint of clinging with its claws. It is likely that in the wild the higher rates of progress indicated above would not obtain, because of difficulties of arboreal travel, lack of maximal stimulus, etc. Fatigue over stretches of a hundred feet or so would also be an important restricting factor, as indicated by the poor condition of animals after 8 or 10 tests on the 12-foot bar. Several fairly effective methods of deslothing the sloth may however be employed, at least to the extent herein described.

It may be questioned whether even a modicum that is praiseworthy attaches to such excitatory tactics practised on the humble sloth. Yet it does appear to be in the nature of man to ever cast about for new stimulants or anti-inhibitors, for himself and his friends, and some observers are driven to test such substances on the animals about them. Fast pacers and night lifers might with profit take a tip from the sloth now and then, however, and consider its ways and perhaps be wise. It may be that a potent sloth extract (*extractum tardigradi!*) would serve a more useful purpose in many ways than excitants, in this present headlong-charging world

The writer is grateful to Dr. H. E. Anthony of the Museum of Natural History, New York, to Dr. G. S. Miller, Jr., of the Smithsonian Institution, Washington, and Dr. R. K. Enders, of Swarthmore College, for some evidence regarding the limits of distribution of sloths. Dr. A. O. Foster and Dr. G. B. Fairchild of the Gorgas Memorial Laboratory have identified a number of sloth ticks, worms and moths, and to

these workers I am also indebted for much information. Mr. J. B. Shropshire, a delightfully keen amateur naturalist of the Canal Zone, supplied considerable data on sloth habits, and through his splendid organizing ability many sloth hunts were arranged and most of our experimental supplies secured.

LIST OF LITERATURE

- ALMEIDA, A. O., and B. DE A. FIALHO. 1924. Métabolisme, température et quelques autres déterminations physiologiques faites sur le paresseux (*Bradypus tridactylus*). *Comp. rend. soc. de biol.*, 91: 1124-1126.
- DE ALMEIDA, M. O. 1928. Sur la régulation nerveuse de la respiration chez le Paresseux (*Bradypus tridactylus*). *Comp. rend. soc. de biol.*, 98: 1573-1574.
- . 1928. Sur la régulation chimique de la respiration chez le Paresseux (*Bradypus tridactylus*). *Ibid.*, 98: 1576-1578.
- ATKILL, L. 1937. Marginal comments. *Spectator*, 158: 514.
- BEHR, W. 1925. Studies of a tropical jungle. *Zoologica*, 6: 5-193.
- . 1926. The three-toed sloth, *Bradypus cuculliger cuculliger* Wagler. *Zoologica*, 7: 1-67.
- . 1938. Personal communication.
- BLUME, W. 1928. Über den Verlauf der Luftröhre bei *Bradypus tridactylus*. *Anat. Anz.*, 65: 230-232.
- BRITTON, S. W., and W. E. ATKINSON. 1938. Poikilothermism in the sloth. *Jour. Mammal.*, 19: 94-99.
- , and R. F. KLINE. 1939. On deslothing the sloth. *Science*, 90: 16-17.
- , and —. 1939. Emotional hyperglycemia and hyperthermia in tropical mammals and reptiles. *Amer. Jour. Physiol.*, 125: 730-734.
- , and —. 1941. In preparation for press.
- , —, and H. SILVETTE. 1938. Blood-chemical and other conditions in normal and adrenal-ectomized sloths. *Amer. Jour. Physiol.*, 123: 701-704.
- BROMAN, I. 1929. Über die angeblich "einzig deste enden" Mesogastrien und Leberligamente bei den Faultieren. *Verhandl. Anat. Ges.*, 38: 58-63.
- BUFFON, G. L. LAC. DE. 1766. *Histoire Naturelle: Quadrupèdes*. 26: 47.
- DE BURLLET, H. M. 1911. Über die äusseren Formverhältnisse der Leber der Faultiere. *Morph. Jahrb.*, Bd. 43, S. 477.
- CORBERGH, H. 1930. Das Organ von Ackerknecht bei Bradypodidae. *Anat. Anz.*, 69: 12-18.
- CUVIER, BARON. 1837. *The Animal Kingdom*. London, 1: 140.
- DAMPIER, W. 1717. *A New Voyage Round the World*. London, Vol. 2.
- EAGLE, E., S. W. BRITTON, and R. F. KLINE. 1932. The influence of cortico-adrenal extract on energy output. *Amer. Jour. Physiol.*, 102: 707-713.
- EXQUEMELIN, O. A. 1678. *De Americacensche ZecRoovers*. Amsterdam.
- FLOWER, W. H. 1882. On the mutual affinities of the animals composing the order Edentata. *Proc. Zool. Soc.*, p. 358.
- GOLDSMITH, OLIVER. 1825. *A History of the Earth and Animated Nature*. New York, p. 442.
- GREW, NEHEMIAH. 1681. *Musaeum Regalis Societatis; or A Catalogue and Description of the Rarities Belonging to the Royal Society, and Preserved at Gresham College*. I., 11.
- HROONER, E., and E. SCHUMAKER. 1928. Some intestinal amoebae and flagellates from the chimpanzee, three-toed sloth, sheep and guinea-pig. *Jour. Parasit.*, 15: 31-37.
- HUEBER, C. H., and G. B. WISLOCKI. 1935. Early development of the sloth (*Bradypus grissus*) and its similarity to that of man. *Pub. Carn. Inst. Wash.* 459: 1-13.
- HOWELL, A. BRAZIER. 1930. *Aquatic Mammals*.
- JUAN, DON G., and DE ULLOA, DON A. 1748. *Relacion historica del viaje a la America*. Tome prim., Cap. V., 135-137.
- KARN, M. C. 1931. Djuka, the Bush Negroes of Dutch Guiana. *New York*. p. 151.
- KREDEL, F. E. 1928. Note on the temperature of the sloth. *Jour. Mammal.* 9: 48.
- LANGWORTHY, O. R. 1935. A physiological study of the cerebral motor cortex and the control of posture in the sloth. *Jour. Comp. Neurol.*, 62: 333-348.
- MILLER, G. S. JR. 1939. Private communication.
- MILLER, R. A. 1935. Functional adaptations in the fore-limb of the sloth. *Jour. Mammal.*, 16: 38-51.

- ORIA, J. 1929. Histiocytos livres no sangue circulante de varias especies brasileiras de mammi-feros sylvestres. *Ann. Fac. Med. Sao Paulo*, 4: 39-48.
- OVIDEO Y VALDÉS G. F. DE. 1526. De La Natural Historia de las Indias: Perico Lijero. Chapter 24, folio 22 (Colophon: "Toledo, 1526").
- PENNANT, T. 1771. Synopsis of Quadrupeds. *Chaster (England)*.
- PURCHASE, SAMUEL. 1613. Pilgrimage. P. 704, note.
- RICHTER, C. P., and L. H. BARTEMEIER. 1926. Decerebrate rigidity of the sloth. *Brain*, 49: 207-225.
- STRAUS, W. L. JR. 1937. Cervical ribs in the woolly monkey. *Jour. Mammal.*, 18: 241-242.
- TEVIS, M. 1925. An animal hanging basket. *Men-sor*, 13: 58.
- TURNER, W. 1873. On the placentation of the sloths. *Trans. Roy. Soc. Edin.*, 27: 71-104.
- WALTER, H. E. 1928. Biology of the Vertebrates. *New York*.
- WEBER, M. 1904. Die Säugetiere. *Jena*.
- WISLOCKI, G. B. 1927. On the placentation of the tridactyl sloth. *Contribs. to Embry., Carn. Inst. Wash.*, No. 380: 209-228.
- . 1928. Observations on the gross and micro-scopic anatomy of the sloths (*Bradypus griseus* griseus Gray and *Choloepus boffmanni* Peters). *Jour. Morph. and Physiol.* 46: 317-397.
- . 1933. Location of the testes and body tem-perature in mammals. *QUART. REV. BIOL.*, 8: 385-396.
- . 1938. The topography of the hypophysis in the *Xenarthra*. *ANAT. REC.*, 70: 451-463.
- , and W. L. STRAUS, JR. 1932. On the blood vascular bundles in the limbs of certain edentates and lemurs. *Bull. Mus. Comp. Zool.*, 74: 1-15.



NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Maud deWitt Pearl, Assistant Editor of THE QUARTERLY REVIEW OF BIOLOGY, 401 Hawthorn Road, Baltimore, Maryland, U. S. A.

BRIEF NOTICES

EVOLUTION

THE MAMMALIAN FAUNA OF THE WHITE RIVER OLIGOCENE. Part II. Rodentia, by Albert E. Wood. Part III. Lagomorpha, by Albert E. Wood. Part IV. Artiodactyla, by William B. Scott. Transactions of the American Philosophical Society held at Philadelphia for Promoting Useful Knowledge. New Series, Volume XXVIII, Parts II, III, and IV.

By William B. Scott and Glenn L. Jepsen. American Philosophical Society, Philadelphia. Part II, \$2.00; Part III, \$1.00; Part IV, \$2.50. 11 $\frac{1}{2}$ x 9; Part II, 155-269 + 11 plates; Part III, 271-362 + 2 plates; Part IV, 363-746 + 44 plates; Part II, 1937; Parts III and IV, 1940 (paper).

The strata of the White River oligocene have been for nearly 100 years the "happy hunting-grounds" of the palaeontologist. Early findings were entrusted to the care of Dr. Joseph Leidy who laid the foundation and gave impetus to the fine quality of work that American palaeontologists have produced. Later, Cope and Marsh developed the collecting of fossil forms to a fine art. Today, many museums are the repositories for the remarkable treasures that were stored so long ago in the White River beds. Leidy, in 1865, listed 14 families and 19 genera as representing the mammalian fauna. Scott in his preface to the Monograph of the White River fauna (cf. Q.R.B., Vol. 12, p. 90 for mention of Part I) lists 35 families and 98 genera of mammalian forms—"yet the

• 'novelties' continue to come in." In Part II of this series (issued in 1937) Wood has increased Scott's list somewhat by his study on the rodents.

In Part III, Wood comes to the conclusion that the lagomorphs (rabbit-like forms) are of a "very ancient mammalian stock, presumably Eutherian, which has evolved, at a slow rate, as an entirely independent line at least since the Paleocene and perhaps since the Mesozoic." There are indications that "for some reason the lagomorphs are a very stable group, genetically, so that mutations of a specializing type take place relatively rarely."

Scott, in Part IV, considers the White River artiodactyls a very ancient and primitive assemblage with but two of the nine families having any descendants in the modern world. One of the striking features is the entire absence of the Pecora. Scott believes that "the Tylopoda took the place of the Pecora and played the role that the latter did in the Old World . . . Of the families included in the Tylopoda, one, the Camelidae, is not questioned by any one and, in the White River genera, there is every reason to think, we have the actual ancestors of all existing camels and llamas."

These studies are enriched by tables of measurements, finely executed text-figures and plates.

THE COURSE OF EVOLUTION *by Differentiation or Divergent Mutation rather than by Selection.*

By J. C. Willis. *The University Press, Cambridge; Macmillan Company, New York.*
\$3.00. 8½ x 5½; viii + 207; 1940.

The ideas propounded by Willis in 1922 in his famous work on age and area have had a great influence on the thinking of the younger generation of biologists. If his views have not been universally accepted *in toto*, the explanation lies in the usual reticence to discard any well-established theory, particularly one that has become literally an article of faith for modern scientists, such as, for example, Darwin's concept of natural selection. Moreover, it is to be admitted that as plausible as Willis's theory is—that evolution results not from natural selection of chance variations but from single mutations which cause structural alterations, and that it proceeds from family to variety—full and final proof of its validity has not yet been given. Additional evidence to support the author's contention is presented in the present volume which constitutes a logical sequence to the earlier work. The author first traces the evolution of his own concepts on the subject of natural selection and describes the kinds of observations that finally led him to the formulation of his theory. He proceeds then to present 34 sets of observations involving frequency of genera, morphology, taxonomy, and geographic distribution. He compares the interpretation of such observations in terms of natural selection and of age and area, respectively, and presents a convincing case for the latter. In the brief space allotted, it is hardly possible to consider adequately the author's discussion. This book, as its predecessor, deserves careful study and will without doubt be the source of a revaluation of current views.



GENES AND GENESIS. *Ministerial Reading Course Selection for 1941.*

By Harold W. Clark. *Pacific Press Publishing Assn., Mountain View, Calif.*
\$1.50. 7½ x 5½; 155; 1940.

Now that the classical Darwinian theory of evolution has been modified by the recent discoveries in genetics it seems that there are only a few minor points that separate the fundamentalist from the natural philosopher. These are expressed by the fundamentalist belief that God created the world in six calendar days. There is nothing, the author asserts, in biology to contradict such beliefs. The arguments used to support this view are not new but the author has brought them up to date by making good use of recent developments. It is well to note that this book is the 1941 selection of the Seventh Day Adventists Ministerial Association. We hope that the ministers will really read it for it is impressive because of the uncommon erudition and dialectic abilities of the author.



STUDIES OF CENOZOIC VERTEBRATES AND STRATIGRAPHY OF WESTERN NORTH AMERICA. *Contributions to Paleontology. Publication No. 514.*

By Paul C. Henshaw, Robert W. Wilson, Hildegard Howard, Alden H. Miller, Jack F. Dougberry and Richard H. Jahns. *Carnegie Institution of Washington, Washington, D. C.* \$2.75 (paper); \$3.25 (cloth). 10 x 6½; iii + 194 + 24 plates + 1 folding map; 1940.

This contribution includes nine studies on the fauna of the Cenozoic from various parts of western North America, eight of which concern mammal remains. The ninth shows the avifauna of Rancho La Brea to be between typical Pleistocene and the typical Recent. Among the faunal lists are descriptions of new species and redescrptions of poorly preserved material, especially that of *Paratylopus cameloides*. There is also a contribution to the stratigraphy of the easternmost Ventura Basin, a description of a new mammalian fauna from Caliente Mountain, studies on the Paramyid rodents and *Pareumys* remains of California, and the mammalian fauna of the Avawatz Mountains. Relationships and correlations are discussed in all these studies.

SOME FOSSIL PLANT TYPES OF ILLINOIS. *A Restudy of the Lesquereux Types in the Worthen Collection of the Illinois State Museum, Augmented by Descriptions of New Species from Mazon Creek. State of Illinois, Department of Registration and Education. Scientific Papers Vol. I.*

By Raymond E. Janssen. *Illinois State Museum, Springfield.* \$1.25. 10 x 6½; xv + 123; 1940 (paper).

The first descriptions of Illinois plant fossils were made in 1866 and 1870 by the paleontologist Lesquereux. He found 109 new species in various localities in the state. Recently 59 of his type specimens have been brought to light and have been restudied and reclassified. The first part of this report deals with the Lesquereux material. Illustrations of his type specimens are shown in 24 photographic plates. In the second part, ten new species and varieties of fossil plant impressions from the Mazon Creek region are described and illustrated. An eleven-page bibliography and an index of species names completes the study.



ON ONE OF THE LEAST KNOWN OF THE CLEVELAND SHALE ARTHRODIRA. *Scientific Publications of the Cleveland Museum of Natural History, Vol. VIII, No. 3.*

By David H. Dunkle and Peter A. Bungart. *Cleveland Museum of Natural History, Cleveland.* 9½ x 6½; 19 + 2 plates (paper).



GENETICS

ANIMAL BREEDING. *Third Edition.*

By Lawrence M. Winters. *John Wiley and Sons, New York; Chapman and Hall, London.* \$3.50. 9 x 6; viii + 316; 1940. This book has been thoroughly revised to present the newer knowledge of scientific breeding gained from recent experience and experimentation. The net income realized on livestock is in direct proportion to the merit of the stock, and high merit can be attained only by an understanding of the biological principles involved in

breeding. With this in mind the author first describes reproductive anatomy, the hormonal control over breeding cycles, the fundamental genetic basis of animal breeding, and detailed procedures for artificial fertilization. The second half of the volume is devoted to the methods used for improving stocks and maintaining them at a high level. This includes purebred breeding, grading, inbreeding, crossbreeding, and community breeding. Not only are numerous examples given as to the efficacy of methods practiced upon domestic animals, but the text also contains reviews of experiments which have already found practical application, and others which hold promise for the future. Animal husbandry has before it the task of devising more adequate measurements of quality and of increasing the use of artificial insemination, proved sires, and records of performance. In addition to its unquestionable value to the breeding industry this book will prove useful in pointing out to animal biologists the fields where research is most demanded. The text is amply illustrated and contains a bibliography of over 400 titles.



AN EXPERIMENT IN THE TEACHING OF GENETICS with Special Reference to the Objectives of General Education.

By Austin DeM. Bond. *Bureau of Publications, Teachers College, Columbia University, New York.* \$1.85. 9 x 6; viii + 99; 1940.

Present day pedagogy stresses teaching the social aspects rather than the systematic foundations of science. The interesting observations reported here bear on the validity of such a viewpoint. Two groups of college freshmen were taught genetics, but in a different manner. For one group, the control, the orthodox textbook exposition was followed. In teaching the other group, the experimental, the question of race differences was especially emphasized. The main results are that in the end the control group demonstrated better knowledge of the mechanics of genetics while the experimental group possessed clearer ideas about

racial problems. These results could have been foreseen but they reinforce the well-known concepts that knowledge of the fundamentals of a science is not sufficient to allow for their general application and that the teacher's viewpoint influences that of the pupil. It will be some time before the new pedagogic technique becomes generally applied and until the final effects are evident it is not proper to prejudge them.



MULTIPLE HUMAN BIRTHS. *Twins, Triplets, Quadruplets and Quintuplets.*

By H. H. Newman. Doubleday, Doran and Company, New York. \$2.50. 8½ x 5½; xii + 214; 1940.

This is the first of a non-technical series of texts published under the auspices of the American Association for the Advancement of Science. Since the book is directed at the general public, Newman has purposely restricted his field of discourse to topics that excite popular interest, as well as misconceptions. He discusses the causes, frequency, and kinds of twins and other multiple births; psychologic traits of and criminality in twins; the scope of studies on twins in relation to the nature-nurture problem. A chapter is devoted to the Dionne quintuplets, and in two other chapters are summarized the results of the well-known investigations of the author and his associates. An excellent list of references is included. As would be expected, the book reflects Newman's authority on the subject. However, this attempt at popular science writing cannot be considered too successful from the standpoint of readability.



PRINCIPLES OF GENETICS.

By E. Grace White. C. V. Mosby Co., St. Louis, Mo. \$2.50. 8½ x 5½; 352; 1940.

The material and scope of this text is much the same as that of several other recent books in the field of genetics, although less technical than some. In addition to the fundamental discussions

of Mendelism, animal breeding, measurement of variation, and eugenics, there are reviews of the most recent work on the nature of the gene and hormone influence. Although the volume is written in a clear and interesting manner, it lacks a critical attitude toward certain studies on which there has been a difference of opinion, particularly in the section concerning human heredity. On the other hand, the writer rightfully discusses the present status of the gene with reservation. The book can well be used in the classroom since its arrangement is orderly, it contains a good topical reference list, and possesses an adequate index.



GENERAL BIOLOGY

FOOD PRODUCTION IN WESTERN EUROPE. *An Economic Survey of Agriculture in Six Countries. Being the Report of an Inquiry organized by Viscount Astor and B. Seeborn Rowntree.*

By P. Lamartine Yates. Foreword by Sir William Beveridge. Longmans, Green and Co., London, New York and Toronto. \$6.00. 9½ x 6½; xv + 572 + 16 plates; 1940.

From 1934 to 1938, series of inquiries into the farming situation in Great Britain were organized by Viscount Astor and B. S. Rowntree. In the course of these investigations it became apparent that the agricultural experience of some neighboring countries in Western Europe, which have a somewhat similar climate to that of Great Britain, might yield some items of great value for the formulation of an agricultural policy in the latter country. Mr. Yates was commissioned to make an intensive study of the conduct of agricultural pursuits in Denmark, Holland, Belgium, France, Switzerland, and Germany. This book, presenting his findings, deals not only with the type of holdings, type of farming (live-stock, dairy, or plant production), proportion of population engaged in agriculture, capital and income of the farm population, land reclamation, cost of food products, etc., but also with market boards, co-operatives, quota systems, and other measures

of control which have grown up in recent years. Each country is considered separately, and in concluding chapters comparisons are made between the agricultural systems and policies of these countries with each other and with Great Britain. The study was concluded before the outbreak of World War II, and the suggestions for future policies will no doubt need revision before the opportunity is presented to put them into effect.

The book is well documented, illustrated with photographs, and there is an index.



ANNUAL REPORT OF THE BOARD OF REGENTS OF THE SMITHSONIAN INSTITUTION: *Showing the Operations, Expenditures, and Condition of the Institution for the Year Ending June 30, 1939. Publication 3555.*

Smithsonian Institution. U. S. Government Printing Office, Washington. \$1.50. 9 x 5 $\frac{3}{4}$; xiii + 567 + 138 plates; 1940.

From a very early date in its history it has been the custom of the Board of Regents of the Smithsonian Institution to enrich its annual report with interesting papers published during the year, which show the more important developments in scientific discovery. The present report is no exception. We regret, as usual, that the limited space in these columns precludes an adequate review, or even a complete list, of the 27 outstanding contributions. The papers of primary interest to biologists include: Humanity in geological perspective, by H. L. Hawkins; Biologic balance on the farm, by W. L. McAtee; On the frontier of British Guiana and Brazil, by H. C. Smith; The sea bird as an individual: results of ringing experiments, by R. M. Lockley (the observations were made at Skokholm Island); Birds and the wind by N. T. McMillan, Captain, Eastern Air Lines (a provocative study refuting some of the ideas accepted by ornithologists concerning the flight and migration of birds); The problem of conserving rare native plants, by M. L. Fernald (he discusses also the introduced exotic plants whose spread has reached weed proportions, thereby crowding out

native plants); Plankton in the water supply, by Florence E. Meier; and several papers of archaeological and ethnological interest. The articles are liberally illustrated with drawings, photographs, or both, and most of them are provided with bibliographies.



LOOK TO THE LAND.

By Lord Northbourne. J. M. Dent and Sons, London. 7s. 6d. net. 7 $\frac{1}{2}$ x 4 $\frac{3}{4}$; v + 206; 1940.

The author believes that many of the economic problems of the present day are conditioned fundamentally by the diseased "biological state" of the world, that is, by the condition of the soil and the conduct of agricultural pursuits. The extent of desert formation has been enormously accelerated in comparatively recent times in the "dust bowls" of the United States, in Australia and Russia which run close to the United States' record in this respect, in Africa, and to a less noticeable but not negligible degree in Europe. This and many other processes of erosion and depletion of once fertile soil the author blames largely on modern farming methods and misdirected research (mass production, specialization of crops or type farming, overstocking in some cases and understocking in others, exclusive use of artificial fertilizers, etc.). He considers also the financial, commercial and sociologic aspects of the problem to the conclusion that a return to the mixed type, self-sufficient farm, with a large, healthy manure pile, and with as little interference from the government as possible, is highly desirable.

The higher the degree of biological self-sufficiency achieved by a farm, a district, or a nation, the more alive, the more vigorous, and the more creative it will be, and the more it will have to exchange with its neighbours, not the less.

Lord Northbourne has a large mixed farm and several market gardens in England, and is actively interested in agricultural education.

A selected bibliography of non-technical works and an index are provided.

MAN AND THE LIVING WORLD.

By E. E. Stanford. The Macmillan Co., New York. \$3.50. 8½ x 5½; xxviii + 961; 1940.

The task of organizing a text for use in the increasingly popular college survey courses in biology is an enormous one, made all the more difficult by the fact that most of these courses are crowded into one semester, and are entirely devoid of any laboratory or field work. Stanford's text is well adapted for just such a course, and presents a program of such scope and variety as to accommodate the needs of widely divergent types of classes and schools. The method of organizing the material into units is an excellent one, making for ease of selection, and resulting in a well-rounded course when the limits of time require that only part of the total field be covered. The textual material is authoritative, well documented, and extremely comprehensive, the latter fact being made clear by ten unit titles, some of which we list: Science and living things; The green plant, manufacturer of foodstuffs and of raw materials for industry; The human body, its structure and functions; Microorganisms and their relation to human life; Domestication and breeding of plants and animals; The biological resources of the United States and their utilization.

The text is supplied with an abundance of illustrative material and a comprehensive index.



BIOLOGY IN THE MAKING.

By Emily E. Snyder. McGraw-Hill Book Company, New York and London. \$2.80. 8 x 5½; xii + 539; 1940.

It is for readers without a scientific background, that this book is written. The author's purpose is "to trace the development of biological discoveries, not as so many facts, but as the product of real men whose lives for one reason or another made them outstanding in their fields." There are several appendices, a chronological table listing the major contributions of the 125 scientists whose works have been discussed, a glossary, a bibliography, and an index.

THIS AMAZING PLANET.

By Roy Chapman Andrews. G. P. Putnam's Sons, New York. \$2.00. 7½ x 5½; ix + 231; 1940.

In *This Weeks Magazine* there has appeared from time to time a series of articles under the general title *This Amazing Planet*. Prepared by the Director of the American Museum of Natural History for popular consumption, they dealt with little-known facts of natural history, prehistoric life, and observations of uncommon behavior of familiar animals, which the author had jotted down on his world-wide travels. These articles, 80 in number, are here made available in book form.



HUMAN BIOLOGY

JOHN AND WILLIAM BARTRAM, *Botanists and Explorers, 1699-1777, 1739-1823.*

By Ernest Earnest. University of Pennsylvania Press, Philadelphia. \$2.00. 8 x 5½; vi + 187; 1940.

This is a biographical essay dealing with two of the more significant figures in American history. Together the lives of the Bartrams, father and son, covered all the eighteenth century and overlapped the seventeenth and nineteenth.

It is a remarkable fact that a man of so little education that he never learned to spell correctly, should have eventually achieved such a pinnacle of eminence that Linnaeus considered him to be the greatest living natural botanist—yet such is the case. To account for this the author has gone deeply into the early environment of John Bartram, and finds that many of the leading intellects of the New World, such as James Logan, Isaac Norris, and Francis Daniel Pastorius, (all of whom were botanists as well as statesmen) were instrumental in shaping Bartram's character. Also, he tells us of numerous botanical gardens in the colonies that antedated Bartram's Arboretum, notably that of Kelpin's, established in 1694 (incidentally, why do we read so little about this picturesque prophet of the frontier?).

It was Logan who was influential in sending the older Bartram to Onondaga in 1743 with Lewis Evans the cartographer

and Conrad Weiser, the interpreter, whose parents were Palatinate refugees, but who was born in America and brought up as a member of the Maqua Indian tribe. The object of this expedition was to make peace between the six nations and some Virginia backwoodsmen. This was the beginning of John Bartram's travels in the colonies and Florida to gather botanical material.

But it was Peter Collinson, the president of the Linnean Society of London, who did most to bring about Bartram's recognition by the scientific world. It was Collinson's mediation that won for Bartram the appointment of Botanist to the King, that induced the other crowned heads of Europe to apply to him for American plants, and that caused all European scholars visiting the colonies to call sooner or later at the Bartram residence.

William Bartram differed in many ways from his father. John believed that the only good Indian was a dead Indian and it was fear of the aborigines (whom he believed to be cannibals) that restricted his travels to the piedmont plateau. On the other hand, William preferred the red man to the white, judging him to have a higher sense of morality and honesty, and he even became initiated into an Indian tribe. Also he had the benefit of the education that his father lacked. He was familiar with the best English literature of his day, particularly with Pope's *Essay on Man*, and his prose journal exhibits such poetic qualities that it was a favorite of Coleridge and Wordsworth, many of whose works show such a striking parallelism of thought to those of Bartram that the author concludes that "Kublai Khan" and "Ruth" might not have been written had not Bartram's *Travels* pointed the way. To appreciate the influence that Bartram may have had on these poets, or on the later naturalists, such as Wilson, Say, and Nuttall one must read this book carefully.

The work is not perfect, however. The consistent misspelling of Ann Mendenhall's name, the use of such an ungrammatical construction as "one genera" and the failure to take into consideration the eleven days disagreement between the

Julian and Gregorian calendars in fixing the birth date of the older Bartram are evidences of slipshod work. A more serious omission is that of all reference to John Bartram's sense of humor. Evidence of this trait of character occurs in the journal of Peter Kalm. It is impossible to read how the Swedish traveler tasted a green persimmon, expressed the juice of *Rhus toxicodendron* between his palms, or threw a club at a skunk to see whether these organisms would really react as Bartram said they would, without getting light on one side of the botanist's character that this book completely overlooks.

A more comprehensive and detailed index would have added to the usefulness of the work.



THE MONGOL EMPIRE: *Its Rise and Legacy*. By Michael Prawdin. Translated by Eden and Cedar Paul. The Macmillan Co., New York. \$5.00. 8½ x 5½; 581; 1940.

A book of absorbing interest. The author has drawn upon his imagination in order to create a continuous and vivid story, yet the substantiation of the main historical facts by chronological tables, a lengthy bibliography, maps, and other data testify to the extensive researches that he has made.

The welding together of the nomadic tribes of Asia into a powerful empire, the extension of that empire into Manchuria, China, India, Asia Minor, and eastern Europe to become the widest empire of all times, all this within a few years and through the great military genius of one man, is a fantastic and almost incredible story. The messenger and spy service, organized in great detail by Jenghiz Khan, had an important part in maintaining his power over the Mongols as well as over the neighboring countries. An "arrow messenger" was regarded as sacred. "The highest prince in the land made room for him to pass when the sound of his horse's bells was heard; and when his mount grew tired, the best available horse had to be supplied." With head and body bandaged to help him endure the long

ride by day and night he rode across steppes and desert "crossing in a few days distances which usually needed weeks to cover." Jenghiz Khan established the framework of a militaristic state where every man enrolled for war or for peace. During times of peace, the hunt, as practised by Mongolians, was simply a training for war, being military in all its phases.

The history of the disintegration of the great Mongolian Empire is even more interesting than its rise to power. In fading away it left its influence in all countries that it had dominated. Particularly was this true of Russia. A descendant of the Khan of the Golden Horde, one of the great Mongolian tribes, became Grand Prince of all Russia, and Tartar nobles intermarried with Russian aristocracy. The easy acquisition by Russia of all northern Asia was the natural outgrowth of this mingling of Russian and Mongolian peoples. Towards the end of the 16th century Cossacks, adventurers, and peasants migrated into the vast plains of Asia to make their homes among the Mongols.

For those desiring a clearer understanding of the historical foundations of eastern Europe and Asia we strongly recommend this book. It elucidates many of the present-day conflicts in the Eurasian setting. A useful index has been provided.



THE TRAGEDY OF GERMAN-AMERICA. *The Germans in the United States of America during the Nineteenth Century—and After.*

By John A. Hawgood. G. P. Putnam's Sons, New York and London. \$3.00.

8½ x 5½; xviii + 334; 1940.

The author, professor of History at the University of Birmingham, has studied the German-American problem for a number of years and spent 18 months in the United States under a Fellowship of the Rockefeller Foundation to do research in the field. The book is divided into three parts: The German as a settler in the United States; New Germanies on American soil; and The significance of the hyphen in German-American history.

Omitting the very early German immigrants and their descendants (this includes the Pennsylvania "Dutch") and those of the past 50 years or so, this scholarly study follows in the main the three classic divisions of German immigration, first outlined by Friedrich Münch: (1) The "German" period from 1815 to about 1855 during which time numerous unsuccessful attempts at founding New Germanies (mostly rural communities) on this continent were made, notably in Wisconsin, Missouri, Illinois and Texas; (2) the period from 1855 to 1870, when the 1848ers, mainly political exiles, realizing that their "cause" in Germany would not succeed and that they therefore would be permanently exiled, turned from old-worldliness, utopian ideas and a passive non-cooperation in American affairs to active participation in political, educational, and journalistic activities in this country. Their opposition to the "No Nothing Party," the Sabbatarian, Prohibition, and, particularly to the Nativism movements (also in some states to slavery) did not add to their popularity and made assimilation difficult. The hyphenated term *German-American*, originated in the early 50's, stuck through (3) the period from 1870 to about 1890, which was characterized by emigrants who left their native land to better their economic conditions, up to the entrance of the United States into World War I.

This is an important sociological study. Many of the 232 items in the bibliography are supplied with notes on their content and viewpoint. There is an index.



MY VANISHED AFRICA.

By Peter W. Rainier. Yale University Press, New Haven. \$2.75. 8 x 5½; viii + 307; 1940.

The author, who was born in Swaziland, South Africa, and is the great-great-grandson of the British admiral after whom Mount Rainier was named, has written the story of his life in Africa, a story that rivals the lustiest of Jack London's adventure novels. Peter Rainier's autobiography is the story of a

seasoned South African adventurer on the lookout for gold, diamonds, ivory, and more adventure; it is the story of a man who knows his country, its resources, and its people. Born in a tent in Swaziland, the author spent part of his childhood in an ox wagon, entering a British school in Natal at the age of nine. This latter proved an irksome thing to a boy who had been permitted by the old Zulu Chief Umfogazana to sit in the ceremonial circle and partake of beer—pleasures extended by Zulu custom only to adults. The Boer War, which was carried on close enough to the classroom to make things interesting, was the only event that saved him from complete boredom during this period. At sixteen he served under Duncan Mackenzie in the Zulu rebellion which took place after the death of the White Queen (Queen Victoria). After that Peter Rainier took Africa in his stride. He searched for diamonds in the Namib desert; went hunting with the Elephant Man, Chris Human; prospected on the Ruenya River, tributary of the Zambezi, for gold; searched in vain for the buried treasure of King Gungunyana; dredged on the Revue River for King Solomon's gold; joined Demilion's troop of scouts in the German Southwest African campaign in 1914; took part in an epic march in which General Duncan Mackenzie led his men on a 300-mile ride in seven days, on one day's rations, to defeat the Germans at Gibeon; was ordered by the Essential Industries Board to Mozambique to speed gold production on the Revue dredge and then to Nigeria for the remainder of the war to construct and operate two tin dredges on the Ropp Tin Mine, Bauchi plateau, where he tamed the Bauchi cannibals for mine work. Then in 1919, he departed, at the ripe age of twenty-nine, for more adventure in the Americas.

There are four text maps as well as maps on the end-papers. A glossary and an index are included.



THE MINGLING OF THE CANADIAN AND AMERICAN PEOPLES. *Volume I. Historical. A Series of Studies Prepared under the Direction*

of the Carnegie Endowment for International Peace, Division of Economics and History.

By the Late Marcus Lee Hansen. Completed and Prepared for Publication by John B. Brebner. Yale University Press, New Haven; Ryerson Press, Toronto; Oxford University Press, London. \$3.00. 9½ x 6½; xxi + 274; 1940.

The relations between the United States and Canada have been characterized in the past by manifestations that are unique in the annals of international sociality. Among these manifestations, and probably the most important, has been the free interchange of populations. In this book, which constitutes the historical section of a demographic survey of the subject, the extent and direction of the more important phases of the population movement between Canada and the United States are described thoroughly and authoritatively. When the colonies were being founded, the westward movement of the people was the same above and below the border. With the revolution began a migration, fostered by the loyalists, from the United States to Canada. After the revolution had subsided the westward expansion in this country at first paralleled that of Canada but later assumed a speedier pace of its own. Coincident with the speeding up of this westward movement there was also a resumption of migration from Canada, as the economic opportunities in the United States became more advantageous. The Canadian migration, in general, exceeded that from the United States to Canada, and, except for some interruptions during the Civil War and World War I, continued until the depression of 1929 and the years that followed. In recent years signs of economic nationalism have developed and the migratory process from either side has virtually stopped. It may be that this situation is only temporary, or, on the other hand, it may manifest the maturity of the two countries. Neither Hansen nor Brebner has attempted to predict the future but in this admirable record of the past they have furnished the necessary groundwork for an understanding of what may occur.

DOCTOR IN ARABIA.

By Paul W. Harrison. *John Day Co., New York.* \$3.00. 8½ x 5½; [10] + 303 + 9 plates; 1940.

Twenty-nine years ago, after graduating from the Johns Hopkins Medical School and interning in a Boston hospital, the author decided to practise medicine in Arabia. This book is the story of his work in Oman, "a tiny opera bouffe empire in the southeastern corner of the Arabian peninsula, an empire of bare rocks, three hundred miles long and a hundred wide." Most of the author's work during his stay of nearly three decades in Arabia was in and about Muttreh, the suburb of Muscat, the latter being the capital of Oman and one of the three hottest places where white men live. Harrison writes most entertainingly of his numerous patients and their way of life—the city merchants, the date gardeners of the Bottina, the oasis Arabs, the Bedouins, the fishermen and Baloochees. He has a keen insight into the problems of the Arabian people. State medicine, he believes, is the only solution to the problem of bringing scientific medicine to the ordinary man in Arabia. "The date gardeners must be freed from malaria, the wandering nomads from Madura foot, the town dwellers from trachoma, syphilis, and gonorrhea. The lepers must be segregated and that dreadful disease eliminated." This narrative has been written with humour and understanding and should appeal to the inveterate travel-book reader. The numerous clinical cases cited and the discussion of the psychology of the Arabian patient should be of especial interest to the physician. There are excellent full-page photographs and one map of Oman and its surrounding territory.



JUNGLE IN THE CLOUDS.

By Victor W. v. Hagen. *Duell, Sloan and Pearce, New York.* \$3.00. 8½ x 5½; x + 160; 1940.

The author, a naturalist, and his wife, Christine, a botanist, journeyed into the high cloud forests of interior Honduras to secure alive, photograph, and study the

habits of the Quetzal, sacred bird deified for centuries by the Mayas and Aztecs. In this book von Hagen entertainingly describes their journey to the Sierra de Sulaco mountains, their sojourn in mountainous inland Honduras, and their successful quest for the King of the Trogons, the Quetzal,

the most beautiful bird in the world. Not much larger than a pigeon, clothed in iridescent plumes quivering from gold to copper to deep jade, with a breast as red as blood hemorrhaging from a deep wound, this bird had given its name to the sweet-tempered god of the Aztecs and its three-foot plumes to the knights of the Plumed Serpent.

The author sent live Quetzals to the Bronx Zoo in New York City and the Zoological Garden in Regent's Park, London, and thereby broke a four-hundred-year-old legend that this bird could not live in captivity.

After the Quetzal hunt the author and his wife journeyed to Montana de la Flor and set up camp on the Rio Guarabiqui to study the ethnology of an "extinct" tribe of Jicaques, compile a vocabulary of Jicaquean words, and explore and photograph the aborigines' stockaded village. A more detailed report on this tribe is to be found in the author's *The Ethnology of the Jicaque Indians*. Following this adventure the author and his wife left for Copan, southernmost city of the ancient Mayan empire and one of the oldest of Mayan cities, to study and photograph the Copan ruins. There are end-paper maps and many excellent photographs.



HUMAN NATURE AND THE SOCIAL ORDER.

By E. L. Thorndike. *The Macmillan Company, New York.* \$4.00. 8½ x 5½; xx + 1019; 1940.

The study of man's social behavior has in general been in the hands of philosophers of the arm-chair variety who have often confused faith with fact. Many biologists who have dealt with the subject have done no better and, of course, neither have many sociologists and psychologists. However, the recent tendency to evaluate quantitatively the action

of groups, to inquire into and measure social behavior characteristics provides a more hopeful outlook for the development of a social biology based on actual observations of overt human activities. Some observations of this kind are summarized and interpreted in this comprehensive treatise. In the first part Thorndike undertakes to delineate and to give a quantitative description of human variation with reference to the more important elements of social behavior including abilities and propensities, wants and their satisfaction. In the second part of the book an attempt is made to relate these characteristics of social variability to group manifestations and institutions (laws and civil regulations, forms of government, public health and welfare, etc.). In this part it is to be noted that the author unfortunately foregoes in places the empirical attitude. Notwithstanding some deviations towards the metaphysical the book on the whole lacks philosophical depth. Even so, and in spite of the inclusion of questionable material, this work represents a great step forward toward a more precise understanding of the social aspects of human biology.



MATTHIAS GISH OF WHITE OAK. *The History of an American Family.*

By J. I. Hamaker. Obtainable from the Author, Randolph-Macon Woman's College, Lynchburg, Virginia. \$3.00. 7½ x 5½; 368; 1940.

White Oak is the name of the community (later changed to Liberty and now known as Penryn) in Lancaster County, Pennsylvania, where Matthias Gish settled with his family circa 1742. He is the founder of the Gisch (or Gish) clan (Dorothy and Lillian are probably the most widely known members) in this country. Primarily a history of this family in Penn's colony, and of the early vicissitudes and wanderings of its members away from the original community into Virginia, Kansas, and to the West Coast, the book is prefaced with a short account of the sectarians (the Brethren, the Mennonites, Dunkards, and Schwenkfelders) in Europe and the United States, and the diary of a journey from

Bertelsdorf, Saxony, to Rotterdam and thence to America made in 1733 by a member of a group of Schwenkfelder refugees. The reader also gets side-lights into the early history of Penn's colony, the family life, education, housekeeping, and food of the early settlers and other matters peculiar to the sectarians in Pennsylvania and the other places where the Gish descendants settled. The book concludes with genealogical material, a bibliography and a copy of the Penn Patent.



A PIONEER DOCTOR IN OLD JAPAN. *The Story of John C. Berry, M.D.*

By Katherine Fiske Berry. Fleming H. Revell Co., New York, London and Edinburgh. \$2.50. 8½ x 6; 247 + 16 plates; 1940.

This biography of a medical missionary to Japan from 1872 to 1894 was written by his daughter. She describes the New England boyhood of her father, his medical training, and his journey with his young wife to the Land of the Mikados at the age of twenty-five. He entered the land at the beginning of the reign of Meiji, the Era of Enlightenment, only a comparatively brief period after the closed Empire had been opened to the world in 1859. The death knell had been sounded for feudalism, and exponents of Western civilization were invited into the land to teach the modern way of life. However, the feudal system did not perish without a struggle and it was a country adverse to the Western World that faced John Berry and his wife. He remained through this period of readjustment, fighting hostility and ignorance. He established the first hospitals and the first nurses' training school, taught the Japanese the science of sanitation, and introduced prison reform and social service work. Marquis T. Okubo compiled a brief biography of him, the first such book to have been written of an American by a Japanese. In addition to the full-page photographs there are many delightful small text illustrations which are redrawings from the works of Hokusai and other artists. A chronological summary of Dr. Berry's life

after 1894 and letters are included in the appendix.



A SURGEON'S LIFE, *The Autobiography of J. M. T. Finney.*

By J. M. T. Finney. G. P. Putnam's Sons, New York. \$3.50. 9 x 6; xiv + 396; 1940.

Doctor Finney (b. 1863, in Natchez, Mississippi) received his medical degree from Harvard in 1884 and immediately was assigned to the Resident Surgical Staff of the Massachusetts General Hospital. At this time aseptic surgery was in the embryonic stage, and the controversy on the respective merits of antiseptic and aseptic methods raged between members of the staff. In 1889 he was called to the newly opened Johns Hopkins Hospital where the planning and construction of the surgical building, operating rooms and accessories had to wait until the question of surgical technique became more stabilized. As Finney has been associated with this hospital ever since, the story of his career parallels the growth of the surgical units from their beginning. His contributions to their development are told with modesty. In addition, Finney tells of his childhood and youth, private practice, his experiences as Chief Consultant in Surgery to the A.E.F., his vacations and recreations, his friends (among them some of our greatest surgeons—the 17 pages devoted to Halsted are fine), and other matters of human interest. His is an interesting story, told with genial humor but freed from the rather blatant calculations at exhibitionism so often found in autobiographies of medical men.



FOUNDATIONS OF AMERICAN POPULATION POLICY.

By Frank Lorimer, Ellen Winston and Louise K. Kiser. Harper and Bros., New York and London. \$2.50. 8½ x 5½; xiii + 178; 1940.

With the possible exceptions of the immigration restrictions and of the few localized attempts to direct migration from

one area of the country to another, the United States has yet to demonstrate any official concern for problems of population. However, if the present political trend continues it is to be expected that eventually some public policy will be formulated. In seeming anticipation the authors briefly and superficially examine the demographic conditions of the country (population, natural resources, health, production, consumption, etc.) and arrive at an outline of the kind of population policy that to them seems desirable. The measures which they advocate are indefinitely stated but in the main involve (a) economic readjustment for certain portions of the population, (b) increased public health and welfare work, (c) spread of knowledge of, and further research on, contraceptive techniques. On the whole, the vague tone and the multiplicity of the propositions advanced seem to indicate that they are not maturely considered or critical views, derived either from an adequate survey of demography or from the history of population policies in other countries and other periods.



THE SEVEN CHARS OF CHELSEA.

By Celia Fremlin. Methuen and Company, Ltd., London. 5s. net. 7½ x 5½; vii + [5] + 178; 1940.

After graduation from Oxford University the author became successively a kitchen-hand, scullery-maid, charwoman in a hospital, maid-of-all-work, milk-bar assistant, and cook-general. The first half of this book gives a lively account of her experiences—not all of the humor and criticism being at the expense of the servant class. In the latter half, deductions are drawn with reference to psychological and sociological aspects, especially on problems of class distinctions in England. The antagonism between classes, the author claims, is artificially produced, and she suggests the historical economic background of the psychological barriers. Little enthusiasm is shown for the Domestic Workers' Union, but it is considered necessary as a means of attacking the symptoms of the present social system.

It offers an inhuman and efficient system instead of an inhuman and inefficient one. . . . The goal before the Union is a state of society in which it will no longer have any place; a state of society in which maid and mistress are of the same class, with the same cultural background and the same education.



WAGES, HOURS, AND PRODUCTIVITY OF INDUSTRIAL LABOR 1909 TO 1939. U. S. Department of Labor. Serial No. R. 1150. By Wirt Bowden. Government Printing Office, Washington. 9 $\frac{1}{2}$ x 5 $\frac{7}{8}$; 28; 1940 (paper).

The original purpose of this study was concerned with wages. The nature of the data collected, however, permitted analyses of related problems, namely: labor productivity and purchasing power, weekly hours, weekly earnings, employment, total wages, and wage earners' share of income paid out.

The years covered by the study were from 1909 to 1939. The industries treated were manufacturing, mining, and railroad transportation. During this period the average hourly earnings rose from 20.7 cents in 1909 to 66.1 cents in 1939. Even with the cost of living taken into consideration the wages of 1939 were 101.5 per cent higher than those of 1909. Average hours of work fell from 51.7 per week in 1909 to 37.8 in 1939. In spite of this, there was a gain in real weekly earnings of 47.0 percent. The details of this and the additional studies reported are given in 8 tables and 6 charts.



THE SU SITE EXCAVATIONS AT A MOGOLLON VILLAGE, WESTERN NEW MEXICO 1939. *Anthropological Series. Field Museum of Natural History. Vol. 32, No. 1. Publication 476.*

By Paul S. Martin, John Rinaldo and Marjorie Kelly. *Field Museum of Natural History, Chicago.* \$1.50. 9 $\frac{1}{2}$ x 6 $\frac{3}{8}$; 97 + 11 maps; 1940 (paper).

This publication comprises the findings of the Field Museum Archaeological Expedition to New Mexico (summer, 1939)

in an early-type Mogollon village in the Apache National Forest in western central New Mexico. The village was named the SU site because of its nearness to the SU canyon and ranch. There is a brief discussion on the Mogollon problem and the existence of the little-known Mogollon culture as a separate third complex of the ancient Southwest. Following this are the descriptions and photographs of seven pit houses, one surface house, the artifacts, pottery, and burials found on the site. In addition there are diagrams of ground plans and sections of the houses, a postulated method of pit-house construction, and a drawing showing the excavated area. The many photographs and well-drawn maps and diagrams serve to make the report an elucidating one for the student of the ancient culture of the Southwest.



TEST TUBES AND DRAGON SCALES.

By George C. Basil in collaboration with Elizabeth F. Lewis. John C. Winston Co., Chicago, Philadelphia and Toronto. \$2.50. 8 $\frac{1}{2}$ x 6 $\frac{1}{4}$; xi + 316; 1940.

Any wide-awake doctor in a foreign land could turn out human-interest stories by the volume, but not many of them could resist, as Basil has, the temptation to assume a superior attitude. The picture of Chungking and the surrounding Chinese hinterland before they became the center of resistance of a resolute people is fascinating. The difference between native ways and those represented by the American hospital marks the meeting of divergent traditions; yet people are much alike everywhere. The suspicious Chinese colonel fundamentally is little different from the indignant U. S. naval commander in similar situations; and the poorest Negroes live just as precariously in Annapolis alleys as do the Chinese squatters outside Chungking's walls. The author's account of his trips into the west and southwest, far from any connection with the occident, are full of color. So are his other stories of places. But one leaves the book with the impression that Basil's chief interest is in China's people.

WHO WALK ALONE.

By Perry Burgess. *Henry Holt and Company, New York.* \$2.75. 8 x 5½; viii + 308 + [4]; 1940.

The central figure—this, incidentally, is not the author, in spite of the fact that the story is written in the first person—is an American soldier who spent some time in the Philippines during the insurrection. Nine years after his return to the United States signs of leprosy appeared. After being treated in New York for a year and showing no improvement, the patient was sent to the leper colony on the Island of Culion in the southern Pacific, where he remained a member of the colony, a hopeless case, for upwards of a quarter of a century. The book gives a picture of the life led by members of the Cape Colony, the fine medical work of the officers and nurses (less than one percent ever contract leprosy), and the various methods used in the treatment of the disease, especially the use of chaulmoogra oil.

Included in the volume are a number of illustrations, an appendix, in which are given questions commonly asked about leprosy and their answers, and an index.

**FAMILY INCOME AND EXPENDITURES.**

Southeast Region. Part 1, Family Income. U. S. Department of Agriculture. Miscellaneous Publication No. 375. Consumer Purchases Study. Urban and Village Series.

By Dorothy Brady, Day Monroe, Gertrude S. Weiss and Thelma Dress. *Government Printing Office, Washington.* 35 cents. 9½ x 5½; v + 389; 1940 (paper).

This study, part of a comprehensive survey to provide data on the way in which American families earn and spend their incomes, covers small-city and village families in the Southeast region of the United States. In order to reduce the number of variables, only families in which the husband and wife were both native-born were studied. White and Negro families were included, but families in unusual situations were excluded. Section 2 deals with village families; Section 3 with small-city families. Fully half the volume is taken up with appendices

which contain much tabular matter. Altogether there are 191 tables in the report.

**LEIF ERIKSON THE LUCKY.**

By F. A. Kummer. *John C. Winston Company, New York.* \$2.00. 9 x 6; 245; 1940.

Although these pages were written primarily for young people, they will delight all readers who appreciate the spirit of adventure. In its personal details the book is fiction, but it is based on historical facts and Norse modes of living of that era. Thus it tells of the government, laws, Yuletide festivities, methods of warfare, shipbuilding, and household activities. Of prime importance in directing Viking exploration was the tide of Christianity, forcing unconvertibles ever westward to Iceland, Greenland, and finally to more distant western shores. Only a small portion of the book deals with these later journeys to our Atlantic coast, as it tells mainly of the adventures of Leif's youth. The customs and courage of the people and their ceaseless struggle against the sea are admirably illustrated in pen and ink.

**FAMILY BEHAVIOR. A Study of Human Relations. Second Edition, Revised.**

By Bess V. Cunningham. *W. B. Saunders Co., Philadelphia and London.* \$3.00. 7¼ x 5½; 527; 1940.

In this second edition (the first edition was reviewed in Q.R.B., Vol. 11, p. 466) the author has augmented the factual bases of her discussion by including new data on changes in family size, economic factors in marriage and family income, and on elements of divorce. The distinctive feature of this work is the excellence of the survey of the literature on the psychological and sociological aspects of inter- and intra-familial relations and the interpretation which the author gives to the reports cited. The biological aspects of the family, however, are not adequately considered. Aside from this shortcoming, which is common to most studies on the

family, this book can be highly recommended as a source of reference for college students.



DERSU THE TRAPPER.

By V. K. Arseniev. Translated from the Russian by Malcolm Burr. E. P. Dutton and Co., New York. \$3.00. 8½ x 5½; vii + 352; 1941.

An entertaining story of travel experiences in the Soviet Far East by the Russian geographer, ethnographer, and geologist, Arseniev. A valued member of the explorer's party was Dersu Uzala, "a primitive hunter who had spent his entire life in the tiagá [forest] and was exempt from all the vices which our urban civilization brings in its train." It was Dersu's resourcefulness and courage that frequently saved the party from disaster in the vast forest of Northern Asia. His wide knowledge of the ways of nature, many glimpses of which the author gives us, immeasurably added to the accomplishments of the three survey parties which Arseniev led, preliminary to the opening up of this vast uninhabited region for settlement and industrialization.



THE CHORTI INDIANS OF GUATEMALA.

By Charles Wisdom. University of Chicago Press, Chicago. \$4.50. 8 x 5½; xiv + 490; 1940.

In this report the author presents a complete picture of the cultural and social organization of the Chorti-speaking Indians, an agricultural people, whose present habitat is in east-central Guatemala, extending at the eastern boundary about ten miles into Honduras to the *municipio* of Copan.

The Chorti area was the locale of the Old Empire Maya civilization of which Copan was the culture center. Excepting the Ladinos, it is now occupied only by Chorti, who may well be direct descendants of the pre-Conquest Copan people and whose language may be fundamentally the same as that spoken at ancient Copan.

There are excellent photographs and drawings. A glossary and an index are included.



OUR SHIFTING POPULATIONS.

By Mark A. Dawber. Joint Committee on Publicity and Promotion of the Home Missions Council and Council of Women for Home Missions, 297 Fourth Ave., New York. 25 cents. 9 x 6; 68; 1940 (paper).

The radio talks in this series, under the general head of *Frontiers of American Life*, were planned to accord with the program of discussion in the 1940-41 meetings of the home mission study groups in the United States. The factual material was gleaned from various sources with which the sociologist is already familiar. The advice to church groups as to what they can do to aid the community solve the problems raised by the presence of migrants, and aiding the individuals of the various migrant groups (sharecroppers, migratory urban workers, "river folk", the migrant Negro, refugees, etc.), smells less high of "uplift" and "religion" than might be expected.



I BOUGHT A MOUNTAIN.

By Thomas Firbank. Countryman Press, Guilford, Vermont. \$2.75. 8½ x 5½; 520; 1940.

This is the story of a young Canadian who, after two years of uninteresting work in a canning factory in Canada, unexpectedly bought a mountain farm when travelling in Wales. It is interestingly written and the general reader will find it entertaining. It is more particularly of interest to the agriculturist in that the main business of farming had to do with sheep raising, of which the fledgling farmer had little knowledge. Firbank's Welsh neighbors, wise by heritage in the care and breeding of sheep, came to his aid. Much of their sage advice concerning the breeding and rearing of sheep is herein reported; also many of the author's failures in this and other lines of farming.

PLOWING THROUGH. *The Story of the Negro in Agriculture.*

By Edwin W. Hullinger. William Morrow and Co., New York. \$1.50. 10½ x 7½; 60; 1940.

Textual matter and numerous illustrations of a propaganda hue, explain how the National Farm Program is seeking to improve the health, the education, and the economic condition of the Southern Negro.



THE FIFTH COLUMN IN WASHINGTON. *Un-Americans on the Government Payroll.*

By Joseph P. Kamp. Constitutional Education League, New Haven, Conn. 25 cents. 9 x 6; 33; 1940 (paper).



ZOOLOGY

THE MAMMALS OF CHINA AND MONGOLIA. *Natural History of Central Asia, Vol. XI, Part 2.*

By Glover M. Allen. *Central Asiatic Expeditions, American Museum of Natural History, New York.* \$10.00. 11 x 8½; xxvi + 730 + 11 plates; 1940.

This fine survey of the natural history of China and Mongolia is destined to become one of the classics in biological literature. During the years 1921-1930 the Central Asiatic Expeditions secured large collections of biological specimens and many photographs. The reports in the different fields are being issued from time to time. When completed they will comprise a series of 12 quarto volumes.

The present volume, the second part of Volume XI (cf. Q.R.B., Vol. 14, p. 85 for mention of the first part) is devoted largely to the typical rodents—the squirrel-like mammals, mouse-like and rat-like rodents, Jerboa-like rodents, and porcupines and their allies. Then follows a much smaller section on the even-toed and odd-toed ungulates, and one on the sea cows. In Volume XI something over 500 mammalian forms are described. The treatise is greatly enriched by the numerous measurements on many forms, aside from the type specimens, which were made

by collectors on fresh specimens in the field. The seventeen preliminary papers by Allen on the material have been embodied in the volume. In Part 1 is given an extensive mammalian bibliography, while Part 2 concludes with a complete index of 57 pages.

In preparing the distribution maps which appear as text figures Allen has taken into account the political changes that have brought about new boundary lines for certain provinces. This must have added appreciably to his labors. In spite of the comprehensive character of the report, Allen states that there are still large areas, particularly in the southern portions of China, yet to be surveyed.



A TEXT-BOOK OF ZOOLOGY. Vol. I. and Vol. II. Sixth Edition.

By the late T. Jeffery Parker and the late William A. Haswell. Vol. I revised by Otto Loewenstein; Vol. II revised by C. Foster-Cooper. The Macmillan Co., New York and London. \$9.00 each. 9½ x 6½; Vol. I: xxxii + 770; Vol. II: xxiii + 758; 1940.

This fine text requires no introduction to biologists. For forty odd years it has been one of the outstanding guides for the beginner. To those who have been nourished on it and who have proceeded into the higher realms of zoology, "Parker and Haswell" will always remain a necessary part of their reference library.

The two volumes first appeared in 1898. Since that time revision has kept pace with changing ideas that the years have wrought. The present edition has been thoroughly revised without in any way departing from the original inductive treatment of the subject matter. Otto Loewenstein, Lecturer in Zoology at the University of Glasgow has revised the first volume; C. Foster-Cooper, now Director of the Natural History Section of the British Museum, the second. Some of the major changes are as follows: the chapter on "General structure and physiology of animals" has been largely rewritten, with new illustrations; all chapters dealing with classification have been thoroughly revised and examples included

to enable the student to ascertain the systematic position of the animals mentioned in the comparative chapter on "General organization"; a new classification of the Fishes is given in which four classes are recognized; the section on Mammals has been enlarged and some extinct forms included. Due to lack of space the sections on Geographical distribution, the Philosophy of zoology, and History of zoology which formed part of the earlier editions have been withdrawn.



INTRODUCTION TO PARASITOLOGY, *With Special Reference to the Parasites of Man. Sixth Edition, Rewritten and Enlarged.*

By Asa C. Chandler. John Wiley and Sons, New York; Chapman and Hall, London. \$5.00. 9 x 6; xiii + 698; 1940.

New advances in the study of parasites have necessitated a revision of Chandler's textbook of parasitology (cf. Q.R.B. Vol. 11, p. 354 for mention of fifth edition). As the title indicates, the sixth edition deals chiefly with the parasites of man, with brief considerations of the more interesting and important species found in lower animals. Discussions of parasites and the diseases they cause include sections on morphology, distribution, biology, pathogenicity, epidemiology, diagnosis or identification, treatment, prevention, and control. With the exception of the two introductory chapters, which deal with history and general biology of parasites, the book is divided into three parts: Protozoa, Helminths, and Arthropods. Classifications of the larger groups, and keys to some of the genera and important species, are printed in small type. Fortunately, the author has included those organisms with uncertain systematic positions: the viruses, Rickettsias, *Bartonella*, and the spirochaetes. A short bibliography is given at the end of each chapter.

Written primarily for college students, the book is an excellent, up-to-date summary of the field, and should be invaluable not only to beginners, but also to teachers, who will find it a useful reference book and guide in their courses.

BIRDS OF THE GREY WIND.

By Edward A. Armstrong. Oxford University Press, London and New York. \$3.50. 8½ x 5½; xv + 228; 1940.

A combination of bird student and poet wrote this interesting collection of stories on the birds of northern Ireland—bird student because the author reveals a wide and constant association with birds that has enabled him to learn many of their habits and mannerisms; poet because these observations are beautifully described in delightful essays which are interspersed throughout with references from the Irish poets, and from the legend and folklore of County Antrim. The love of the author for his country and its birds is manifest all through the book by his nostalgic portraiture of field, mountain, and lough.

The merganser, the swan, the oyster-catcher, the cuckoo, the short-eared owl, are but some of the birds with which the author has become well acquainted and of which he writes more fully. There is much good ornithological material to be garnered from these pages; the author believes that birds are more plastic in their behavior than is commonly held, and in order to interpret their actions and reactions in a better manner, the observer should watch with something more than cold scientific objectiveness.

The bird photographs, some taken by the author and others by his friends, are excellent and deserve special commendation.



THE CHILDHOOD OF ANIMALS.

By Sir P. Chalmers Mitchell. Penguin Books, Harmondsworth and New York. 25 cents. 7 x 4½; 243; 1940 (paper).

The author, besides being Secretary of the Zoological Society of London for more than 30 years, was also the creator of Whipsnade Zoological Park. This zoo emphasizes the natural environments of animals instead of the usual cages of stone and iron bars. For this reason he has had excellent opportunity to study animal life under more or less natural conditions and, as a trained professional zoologist, has

observed and recorded the habitats of many wild animals whose life histories are little known.

The book is limited to the childhood of animals, gleaned not only from observations in the park, but also from the literature and experiences of others. The duration of youth, the color patterns of the young, the limitation of families, brood-care, food and taming of the young, are but some of the subjects ably recounted. Emphasis is on birds and mammals although other vertebrates and many invertebrates are included to round out the discussions. In many places the author inserts his own ideas and interpretations, all of which are well made and in many cases, most stimulating. A thoroughly delightful book, well written and authentic.



ZOOLOGICA. *Scientific Contributions of the New York Zoological Society. Volume XXV, Part 3, Numbers 19-24.*

New York Zoological Society, Zoological Park, New York. \$1.10. 10½ x 7; 87 + 4 plates; 1940 (paper).

The following papers are contained in this number: Eastern Pacific Expeditions of the New York Zoological Society. XX. Medusae of the Templeton Crocker and Eastern Pacific Zaca Expeditions, 1936-1938, by Henry B. Bigelow (20 text-figures); Two new species of Trematodes (*Apharyngostrigea bilobata*: Strigeidae, and *Catbaemasia nycticoracis*: Echinostomidae) from herons, with a note on the occurrence of *Clinostomum complanatum* (Rud.), by O. Wilford Olsen (1 plate); Nesting of the sunfish, *Lepomis auritus* (Linnaeus), in tidal waters, by Neil D. Richmond (1 plate); Eastern Pacific Expeditions of the New York Zoological Society. XXI. Notes on Echinoderms from the west coast of Central America, by Hubert L. Clark (2 plates, 4 text-figures); The nesting behavior of *Empomoris gibbosus* (Linnaeus) in a small pool, by C. M. Breder, Jr. (2 plates, 2 text-figures); Reproductive activities of a hybrid minnow, *Notropis cornutus* × *Notropis rubellus*, by Edward C. Raney.

MOSQUITO CONTROL. *Practical Methods for Abatement of Disease Vectors and Pests. By William B. Herms and Harold F. Gray. The Commonwealth Fund, New York; Oxford University Press, London. \$3.50. 10 x 6½; xii + 317 + 23 plates; 1940.*

This book has been written with the needs of engineers, physicians, and entomologists in mind.

It is intended to be a practical handbook on mosquito abatement, not a textbook on drainage engineering or a technical monograph on entomology. It endeavors to present the fundamental principles of mosquito control, emphasizing practical application, geographic variation, and ecological differences in sufficient detail to indicate the main methods of attack on the problem. . . . References to the literature are intended to be representative rather than exhaustive.

A wide range of topics is included: education of the public, state laws, breeding places of mosquitoes, drainage and reclamation, oils, larvicides, and the economic aspects of this phase of public health work. The usefulness of such a book is obvious; it should find ready welcome by those engaged in such activities.



WINGS AT MY WINDOW.

By Ada C. Govan. Illustrated by Dorothy Bayley. The Macmillan Co., New York. \$2.50. 8 x 5½; xiv + 198; 1940.

A chickadee landed on the window sill near a bed-ridden mother and thereby started a remarkable tale. Inspired by this visitor, the patient started to feed the bird and then there shortly evolved a huge program of bird feeding and observing that culminated first in the patient's recovery both in body and soul, and second, into a bird banding station that produced some interesting ornithological records.

Recorded herein are the courtship antics of numerous birds, especially that of the purple finch. Some banding records of rose-breasted grosbeaks, other acute observations on bird behavior all add to make this book interesting and in some respects valuable. The professional ornithologist may be displeased with the subjectiveness of the author's observations and interpretations, but then the book was not written to replace a text.

ESSENTIALS OF ZOOLOGY, *Emphasizing Principles of Animal Biology.*

By George E. Potter. C. V. Mosby Co., St. Louis, Mo. \$3.75. 8½ x 5½; 526; 1940.

With the help of several biologists, Potter has organized an excellent text for use in a college course of general zoology. Aiming at a well-rounded course, he has stressed not only the essentials of taxonomy, anatomy and physiology of a representative member of each phylum of animals, but has included pertinent discussions on animal genetics, animal anomalies, animal ecology, and evolution.

The logical organization of the textual material, the abundance of well-chosen illustrations, the detailed table of contents, the glossary, and the complete index, as well as the new eye-tone paper on which the text has been printed, are all factors which point to the high quality of this volume.

**PLANT GALLS AND GALL MAKERS.**

By E. P. Felt. Comstock Publishing Company, Ithaca. \$4.00. 9 x 5½; viii + 364; 1940.

The author's *Key to American Insect Galls* which was published as the New York State Museum Bulletin Number 200 in 1917, and of which the supply has long since been exhausted, here appears in a rewritten and extended version. The section on gall wasps on oaks, especially, has been extended to include the important contributions and a long series of photographs made by A. C. Kinsey and L. H. Weld.

Part I (35 pages), serving as introduction, discusses gall types, the principal gall-producing insects and their biology, alternation of generations, economic importance, the various ways in which galls are developed, and methods of collecting them. Part II gives a list and classification of the galls, arranged according to plant host. This part is generously illustrated with photographs and drawings.

Technical terms have been avoided as much as possible in order to bring this exhaustive work within the appeal of the

interested general reader, but its value to the specialist is not thereby reduced. A short bibliography and an index are appended.

**THE CONTROL OF ORGANISMS.**

By Frederick L. Fitzpatrick. Bureau of Publications, Teachers College, Columbia University, New York. \$2.75. 8½ x 5½; xi + 334; 1940.

The organisms referred to in this title are those commonly designated "pests." Some of them convey diseases, some cause diseases, both in man and his domesticated beasts of burden, others attack his crops, while still others invade his home and wreak devastation among his books, furniture, and clothing.

The natural history of all such economically significant organisms is set out in detail, with instructions for combating them, and in addition the history of man's effort to combat disease from the days of Hippocrates to those of Ehrlich. Without this the book would be dry reading indeed.

The index covers twelve pages, but the bibliography is painfully short, and even the author's apology does not compensate for its brevity.

**INTRODUCING INSECTS. *A Book for Beginners.***

By James G. Needham. Illustrations by Ellen Edmonson. Jaques Cattell Press, Lancaster, Penna. \$1.50. 7½ x 5½; v + 129; 1940.

The purpose of this little volume is to acquaint the general public with insects, both good and bad. The textual material includes discussions of the identifying characteristics, the life histories, and the economic importance, as well as the best methods of control of a number of our common insect pests. For anyone whose interest in insects extends beyond that of simply wanting to read about them, there are several chapters dealing with the materials and techniques of collecting and rearing them. The book is written very

simply, in non-technical language. It is well supplied with illustrative material and carries both a brief table of contents and an index.



FISH PRODUCTION.

By Josephine Perry. Longmans, Green and Co., New York and Toronto. \$1.50. 8 x 5½; 104; 1940.

The many techniques and materials used in fishing have made for great specialization. Thus the fisherman versed in the use of a net is seldom competent at line fishing; the trawl fisherman will seldom be proficient at shore fishing. This book gives, in simple language, the details of the methods used in the various divisions of the fishing industry. A short chapter on fish hatcheries and fish conservation is also included. The book was written, as stated by the author, "to interest young grade-school students in an important national industry of which little is known". The volume well fulfills this aim. It is profusely illustrated and an index is appended.



AMERICAN SONGBIRDS.

By Maitland A. Edey. Random House, New York. \$1.00. 11 x 8½; 72; 1940.

The most attractive feature of this book is its low price, a fact that will enable any young bird student to own a well-illustrated guide to our native (eastern North America) songbirds. The color plates are those of Fuertes that first appeared in the *Birds of New York*. It is too bad that the illustrations could not have been printed a little more carefully, aside from the fact that they show wear. The text material is limited to a few descriptive notes on the 108 species herein considered and a brief introduction to bird study.



POMATOCEROS, SABELLA AND AMPHITRITE. L. M. B. C. *Memoirs on Typical British Marine Plants and Animals*, XXXIII.

Edited by R. J. Daniel. Department of Oceanography, University of Liverpool.

By Joan G. Thomas. University Press of Liverpool, Liverpool. 12s. 6d. net. 9½ x 6; vii + 88 + 11 plates; 1940.

This memoir consists of an anatomical report on three species of sedentary polychaetous worms, *Pomatoceros triqueter*, *Sabella pavonina*, and *Amphitrite johnstoni*. It is pointed out how the peculiarities of these three worms are correlated with their specialized mode of life. Numerous plates illustrate the somewhat technical text material which includes the major anatomical systems and brief notes on development.



HONEYCRAFT in Theory and Practice.

By J. A. Lawson. Diagrams by Audrey Lawson. Chapman and Hall, London. 3s. 6d. net. 7½ x 4½; xii + 228; 1940.

This is a "cheaper edition" of a well-known British book on bee-keeping which was first published in 1931. It is "a severely practical book", as the author meant it to be. It is abundantly illustrated, and nothing pertinent to the subject seems to have been omitted. Yet the book is succinctly and exceptionally well written. The author is a Fellow of the Royal Entomological Society.



CHILDREN OF THE SEA.

By Wilfrid S. Bronson. Harcourt, Brace and Co., New York. \$2.00. 8½ x 6½; [8] + 264; 1940.

This is a book for children. It is the story of a porpoise and the pickaninny that made friends with it. The illustrations are artistically executed.

While the book has no special scientific value, it is scientifically accurate. It has more in common with "Peter Rabbit" than with "Uncle Wiggly Longears." It is imaginative fiction of the better type.



INDEX-CATALOGUE OF MEDICAL AND VETERINARY ZOOLOGY. Part 4. Authors: D to DŽUNKOVSKI. U. S. Department of Agriculture.

By Albert Hassall, Mildred A. Doss, Ruth M. Taylor, Gertrude B. Carson and Dorothy Bero. Government Printing Office, Washington. 30 cents. $9\frac{1}{2} \times 5\frac{1}{2}$; 961-1176; 1940 (paper).

Mention has already been made in these columns of the earlier parts of this revised index-catalogue [cf. Vol. 13, p. 468 (Parts 1 and 2) and Vol. 15, p. 96 (Part 3)]. As in the earlier numbers the index section is preceded by a list of abbreviations for libraries and for serial publications. We again call attention to the biologist of the usefulness of this index.



BOTANY

ILLUSTRATED FLORA OF THE PACIFIC STATES, Washington, Oregon, and California. Vol. I. *Opbioglossaceae* to *Aristolochiaceae*. Ferns to Birthworts.

By Leroy Abrams. Stanford University Press, Stanford University; Oxford University Press, London. \$7.50. $10\frac{1}{2} \times 7$; ix + 538; 1940.

This monumental work is to appear in four volumes. Volume I, dealing with ferns to birthworts (1299 species), was first issued in 1923 but the paper upon which it was printed was unsatisfactory. A reprinting, with some revision, has now been made on a paper of lasting qualities. The publishers announce that copies of the 1923 printing will be accepted for \$3.00 credit toward the purchase of a new copy.

The three Pacific states, roughly 1,300 miles in length and 250 miles in width, traversed by two great mountain systems, and possessing a widely divergent rainfall, furnish conditions for an extensive flora of great complexity. There are sound reasons for the belief that in temperature the climate of the coastal region of the present time has changed but little from what it was in the Cretaceous Period, the Pacific ocean having served throughout the ages as a great thermostat. Thus the climatic conditions and the physical barriers would account for the large numbers of endemic genera and species of plants. The presence of the boreal plants in the high mountain ranges, far from

their normal habitat is probably due, in part at least, to the Glacial Period, while the flora of the Great Basin and Mexican elements have pushed in from the east and south.

The *Illustrated Flora* is designed to be a comprehensive reference work, describing and illustrating every species of fern, flower, tree, and shrub known to grow wild in the area. In designating distribution, Merriam's system of Life Zones has been used, since geographical distribution by states is quite inadequate. The table of contents is arranged first according to the scientific names of the families, followed by a second arrangement according to the English names. An index to generic and family names completes the volume.

While of special interest to the student of botany, everyone interested in the native plant life of the Pacific States will find this work a valuable handbook.



TEXTBOOK OF BOTANY.

By E. N. Transeau, H. C. Sampson and L. H. Tiffany. Harper and Bros., New York and London. \$4.00. $9\frac{1}{2} \times 6\frac{1}{2}$; xi + 812; 1940.

A traditional query (vocalization often repressed) of beginning students in a science is, "But what does all this stuff mean to me?" The authors answer this question by a departure from the standardized, not to say dull, method of plunging the student into a maze of classification and morphological characteristics. Instead, most of that "stuff" is brought out in ecological considerations which reveal just how vital the study of botany is to the welfare of man. Next in importance is the thorough treatment accorded plant physiology and the interrelationship between structure, function, and environment. The most recent advances of scientific research in both ecology and physiology are incorporated in the volume. In addition to descriptions of the various components of typical plants, the fungi, bacteria, mosses, ferns, and underwater plants are also discussed. A considerable

section is devoted to heredity and a chapter to plants of past ages.

The book will probably prove most useful as supplementary reading since its arrangement may not conform to most teachers' established order of presenting the material. Each chapter is concluded with a list of references. A thorough index is provided.



CHINESE HOUSES AND GARDENS.

By Henry Inn. Edited by Shao Chang Lee.

Fong Inn's Limited, Honolulu. \$5.00.

12 x 9; xii + 140; 1940.

Mr. Inn, a resident of Honolulu and a student and collector of Chinese art, spent a number of years traveling in China, photographing Chinese homes and gardens, and drawing designs of details which did not lend themselves well to photography. Urged by his friends to publish them in book form, he secured the collaboration of Mr. Lee and several other eminent authorities on Chinese life and art in writing the five articles of which the first part of the book is composed. The second part consists of photographs of parts of homes and gardens and detailed drawings by the author of window grills, panels, railings, benches, etc. As many of the homes and gardens portrayed have been damaged or completely destroyed by the war, we have in this beautiful book an important record of Chinese architecture and gardens. Landscape architects, gardeners, and interior decorators will find much of interest and of practical value in the photographs and drawings.



ELEMENTS OF BOTANICAL MICROTECHNIQUE.

By John E. Sass. McGraw-Hill Book Co.,

New York and London. \$2.50. 9 x 6;

ix + 222; 1940.

The need for a text which would include all the pertinent knowledge and essential techniques for collecting, preserving, staining, embedding and sectioning botanical material for microscopic study has been the underlying stimulus for the preparation of this volume. As an authority

in both botany and microtechnique, Sass is well qualified for writing such a book. In addition to the general techniques employed in the preparation of various structures of the four phyla of plants for study under the microscope, the author has included several chapters dealing with the criteria for successful processing, the preparation of whole mounts, the construction, use and care of the microscope, and some worthwhile suggestions for successful photomicrography. The text is well illustrated and carefully indexed.



MANUALE DI PATOLOGIA VEGETALE.

By Raffaele Ciferri. Società Anonima Editrice Dante Alighieri, Genova, Roma and Napoli. 50 Lire. 9 x 5½; xxiii + 730; 1941 (paper).

This manual has been prepared to fill a long-felt need in Italian scientific literature for an adequate didactic treatment of plant pathology, and for use in Italian universities. It is marked by its clear and relatively brief critical discussions of various arguments raised in the more recent literature on the subject, and by numerous references to phytopathological contributions in Italy and elsewhere that have been advanced in the study of plant diseases. After a complete historical and analytic development of the subject from antiquity to the present the author progresses to more specialized phases: diseases and changes produced by non-parasitic causes; virus diseases; diseases caused by cryptogamic parasites; mixothallophytic diseases; fungous diseases; and the phanerogamic parasites. An appendix on checking grass infections is included. The work is profusely illustrated with drawings and photographs; it is well annotated, and indices to authors and subjects have been added.



SHRUBS IN THE GARDEN AND THEIR LEGENDS.

By Vernon Quinn. Illustrated by Marie A. Lawson. Frederick A. Stokes Co., New York. \$2.50. 8 x 5½; x + [2] + 308; 1940.

A companion book to Miss Quinn's *Stories and Legends of Garden Flowers*. In an interesting and informal manner she writes of thirty of the most popular garden shrubs, devoting a full chapter to each. She describes the most desirable species and varieties, tells their history and legends and folklore about them. Here and there between legends and folklore are valuable bits of information concerning the culture of the shrub and its uses in the planting scheme.

Amateur and professional gardeners alike will find this book worthy of their attention, and the general reader will find it interesting. The text is profusely illustrated and interpreted with drawings by Marie A. Lawson. There is an index of both botanical and common names of the shrubs and a table grouping them into orders and families.



THE HOME GARDENING ENCYCLOPAEDIA.

Edited by Walter Brett. Chemical Publishing Co., New York. \$2.50. 8½ x 5½; 448 + 8 plates; 1940.

This encyclopaedia contains a wealth of practical information for the gardener both in England where the book was written, and in this country. However, much of the information will need to be adapted to the varying climatic conditions of our country. The month by month planting calendar is of doubtful value to gardeners here. Some of the suggestions for the control of pests are rather quaint. Even the most ardent gardener in the United States would hardly "dig up some worms, take them to a chemist, and ask him to impregnate them with poison", to be used as mole bait.

The volume has thirty reference charts, eleven illustrations showing practical gardening operations, and eight color plates of garden plants.



AMERICAN WILD FLOWERS.

By Cecile H. Matschat. Random House, New York. 50 cents. 10½ x 8; [28]; 1940.

A picture book and not a detailed guide to American wild flowers. It is outstanding for its beautiful full or half-page color plates of eighteen wild flowers. Accompanying each plate is a short text. The inside covers contain small green and white drawings and short notes on twenty-four additional wild flowers. A list of the wild flowers illustrated and arranged according to their season of bloom is included. The book should be helpful to teachers of nature study, scoutmasters, camp counselors, and librarians of juvenile literature.



THE FERNS AND FERN ALLIES OF WISCONSIN.

By R. M. Tryon, Jr., N. C. Fassett, D. W. Dunlop and M. E. Diemer. Department of Botany, University of Wisconsin, Madison. \$1.00. 10 x 6½; v + 158; 1940.

A total of 118 species, varieties, forms, and hybrids of ferns and fern allies known to grow in Wisconsin are described. The ferns are represented by three families—the *Polypodiaceae*, *Osmundaceae* and *Ophioglossaceae*; and the fern allies by five—the *Salviniaceae*, *Equisetaceae*, *Lycopodiaceae*, *Selaginellaceae* and *Isoetaceae*. The descriptions, drawn from herbarium specimens, consist of short characterizations. The book is profusely illustrated with photographs, drawings, and maps showing the localities where the species or varieties have been found. A glossary and an index, giving both scientific and common names, have been provided.



STUDIES OF CENTRAL AMERICAN PLANTS—I. *Field Museum of Natural History, Botanical Series, Volume 22, Number 4.*

By Paul C. Standley and Julian A. Steyermark. Field Museum of Natural History, Chicago. 75 cents. 9½ x 6; 103; 1940 (paper).

This report is devoted principally to descriptions of new species of Guatemalan plants, to notes regarding species new to the country, and to those of rare occurrence in Guatemala or in other parts of their range. The data given here represent

only a small part of those worthy of report, and additional matter will be published later.



UNIVERSITY OF COLORADO STUDIES. *Series D. Physical and Biological Sciences, Vol. I, No. 2.* Containing the Following Articles: *Magnetic Double Refraction*, by Frank E. E. Germann and Charles F. Metz; *Colorado Rusts of Woody Plants*, by Paul F. Shope.

University of Colorado, Boulder, Colorado.
\$1.00. 10 x 6½; 57; 1940 (paper).



MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Publication No. 518. Volume XXVIII, Nos. 170 to 178.*

Carnegie Institution of Washington, Washington, D. C. \$4.00 (paper); \$5.00 (cloth). 11½ x 9; iii + 451 + 34 plates; 1940.

The present issue of this valuable series contains the following papers: (1) Growth and development of the chimpanzee, by A. H. Schultz. This study is based on monthly measurements on two chimpanzees of different sex (the male was measured for a period of 4 years; the female, for ½ years), something over 100 preserved or fresh bodies, and 90 skeletal specimens. Of great value were the fetal and new-born animals. The paper includes much tabular material, 11 figures, and 3 plates. (2) The placentation of *Procavia capensis* with a discussion of the placental affinities of the Hyracoidea (7 plates, 1 graph), by G. B. Wislocki and O. P. van der Westhuysen. Eighteen pregnant uteri, 8 of which consisted of graded stages of embryos from the limb-bud stage up to fetuses of 70-90 mm. crown-rump length, formed the basis of this work. (3) Growth in vitro of ovarian germinal epithelium (two plates), by J. Herman Long. Whole new-born mouse ovary rather than fragments of adult mouse ovary yielded the best results. (4) Development of the neuro-

muscular spindle in human fetuses (4 plates), by Fidel Cuajunco. The ages of these fetuses were from 10 to 15 weeks, and older. (6) Studies of the reproductive system of the alligator. IV. Observations on the development of the gonad, the adrenal and the Müllerian duct (4 plates), by T. R. Forbes. (7) A volumetric analysis of young human embryos of the 10- and 12-somite stage (4 plates [2 colored] and 6 text figures), by E. A. Boyden. (8) Defective development of the cerebral cortex involving symmetrical bilateral areas (3 plates), by P. A. M. F. Fitz-Gerald. (9) Menstruation in intraocular endometrial transplants in the rhesus monkey (7 plates, 1 text figure), by J. E. Markee. (10) The maturation of "excitability" in the precentral gyrus of the young monkey (*Macaca mulatta*) (33 text figures), by Marion Hines and E. P. Boynton. Literature lists accompany each paper. As is always the case with these publications, the illustrations are very fine.



DEVELOPMENTAL ANATOMY. *A Textbook and Laboratory Manual of Embryology. Fourth Edition, Revised.*

By Leslie B. Argy. W. B. Saunders Co., Philadelphia and London. \$6.75. 9½ x 6½; ix + 612; 1940.

As a result of a policy of the author not to revise his book until major additions and improvements could be offered, the present volume represents almost a complete change from previous editions (cf. Vol. 6, p. 242, and Vol. 10, p. 110 of this Review). We now have an authoritative work encompassing the latest developments culled from the world literature on embryological research. The combined references, appended to the chapters, total over 600.

Part I features the germ cells and fertilization, cleavage, germ layers, placentation, and general considerations as to growth and external form. The main body of the text concerns organogenesis, subdivided according to the three germ-layer derivatives. Throughout the book the reference is to human development except where a point may be clarified by

introducing phylogenesis or the embryology of some other mammal. The discussion of each organ contains an account of anomalies that frequently occur.

The laboratory manual details the development of successive stages in the chick and pig embryos, giving adequate instructions for the techniques to be employed in examining each. This section is a decided improvement over the corresponding material in earlier editions. In the book as a whole, 450 drawings and a number of tables have been added. The index covers twenty-five triple-columned pages.



BAILEY'S TEXT-BOOK OF HISTOLOGY. Tenth Edition.

Edited by Philip E. Smith, Russell L. Carpenter, Wilfred M. Copenhaver, Charles M. Goss and Aura E. Severinghaus. William Wood, Baltimore. \$6.00. 9 x 5½; xviii + 764; 1940.

No feature which has made Bailey's *Histology* such a widely accepted text and reference through nine previous editions has been subtracted from the present volume. It remains a detailed and authoritative description of the tissues of the several organ systems. Preceding the systematic survey are chapters on the fundamental structural unit of all living matter, the cell, and also an entirely new section on the salient features of developmental anatomy. More detailed descriptions of organo-genesis are presented at the conclusion of each organ or system studied.

Although the book has been revised and brought up to date throughout, the principal alterations have occurred in the description of nervous tissues. A brief chapter on organization has been added, and the discussion of the central nervous system has been somewhat shortened.

Probably the main feature which has given this volume such vitality is that it treats histology as a vital subject. Structure is considered always in relation to physiological activity. Since pathological conditions can be understood only with a thorough background of normal

structure and function, this book will prove of great value to students and practitioners. In the present edition selected references have been added to each chapter and there are a number of new illustrations.



THE MICROSCOPIC ANATOMY OF VERTEBRATES. Second Edition, Thoroughly Revised.

By James I. Kendall. Lea and Febiger, Philadelphia. \$3.75. 9½ x 5½; 342; 1940.

This book is intended to present to college students a working knowledge of vertebrate microscopic anatomy. The book meets its purpose in that the text is simple, didactic and well-illustrated. It might have indulged with great profit, however, in the luxury of at least some slight discussion of current problems in the field, particularly those that concern the correlation of structure and function. The illustrations are simplified—perhaps too much so in some cases—but not well-labelled. The chapter on technique may be helpful to beginning students. The list of titles in the bibliography is taken exclusively from recent American periodicals. It is unfortunate that the excitement of many of the provocative titles does not find its way into the text.



ATLAS OF OUTLINE DRAWINGS OF THE DOGFISH SHARK, THE NECTURUS, AND THE CAT FOR VERTEBRATE ANATOMY.

By Samuel Eddy, Clarence P. Oliver and John P. Turner. John Wiley and Sons, New York; Chapman and Hall, London. \$1.50. 11 x 9; [6] + 77 drawings; 1940 (paper).

This volume contains many good outline drawings of the organ systems of various animals used in the laboratory and is supplementary to the laboratory manual (cf. Q. R. B., Vol. 15, p. 249) by the same authors. The drawings are fortunately unlabeled, thereby enabling the student to exercise a little ingenuity.

PHYSIOLOGY AND PATHOLOGY

THE UNIVERSE THROUGH MEDICINE.

By J. E. R. McDonagh. William Heinemann (*Medical Books*), London. 25s net.

9½ x 7½; v + 389; 1940.

The title of the book does not overstate the author's ambitious undertaking. There is a prologue and an introduction, followed by six chapters called respectively, the First, Second, Third . . . Sixth Circles. The subheadings of these chapters are: From the beginning of activity undergoing condensation of the birth of the atom: From the birth of the atom to that of the molecule; Chemical combination; The colloid state; The vegetable kingdom; The animal kingdom. There is an epilogue and a bibliography of 44 book references but no detailed literature citations.

In the introduction the author states: "My studies in this field [skin and venereal diseases] led me to conclude that most of the so-called 'skin diseases' are manifestations of disease caused by what I term 'intestinal toxæmia.'" The author is untrammelled by established definitions or by the limitations of experimental technique or by the results of experimental studies. Such terms as hydration and dehydration are used repeatedly in ways which mystify the biochemist as to his meaning. The following quotations selected at random will serve to give the prospective reader an idea of the flavor of the book:

The interaction between opposing products I refer to as "inter-particular disharmony" in contra-distinction to the "intra-particular disharmony" which may occur between the bricks in a product.

"Activity" is the name I give to the form of matter others call "energy." Calcium functions as a radiator and completes a cycle of chemico-physical changes with sodium, for it is the janitor to the dehydration which the protein particles undergo and consequently is the guardian of regress.

The main natural function of the seventeenth element [chlorine] is that of binder, as it connects sodium to the protoplasm of cells and to the protein particles in the plasma and potassium to the nucleus of cells and to the red blood-corpuscles.

The phosphorus individual is tall, thin, nervous and susceptible to external impressions. This element in potency is useful in the last stage of an acute illness such as pneumonia, for example.

Such quotations could be extended to hundreds. The entire book suggests the

language of the astrologer rather than that of the scientist. The author is to be commended for his sustained energy, vivid imagination and enthusiasm.



OBESITY AND LEANNESS.

By Hugo R. Rony. Lea and Febiger, Philadelphia. \$3.75. 9½ x 6; 300; 1940.

In the preface the author points out that although the scientific literature of obesity and leanness is rich in papers dealing with the various pathological and clinical aspects of the problem, as well as with summaries and reviews of the available material, no comprehensive presentation of the subject has appeared since v. Noorden's monograph on obesity in 1900. All who are aware of the extent and nature of this literature are aware that during the past forty years many new facts have emerged which show that obesity and leanness involve more than a balance between caloric intake and output.

In this scholarly discussion of the literature the author gives an excellent account of the physiology of fats and adipose tissue. Then the pathogenesis of obesity and leanness is discussed under the following chapter headings: The caloric balance; The endocrine system; The nervous system; The intermediary metabolism; Lipophylia; Heredity; and a Résumé; the homeostatic body weight regulation. Part III treats the clinical aspects of obesity and leanness. Froehlich's syndrome, the pineal syndrome, Cushing's syndrome, Dercum's disease, Laurence-Biedl disease, Schueller-Christian syndrome, Morel syndrome, and v. Gierke's syndrome are discussed from the basis of diagnostic procedure. Other chapter headings in this section are: Clinical pathology of obesity; The therapy of obesity; Classification and diagnosis of leanness; The therapy of primary leanness.

The author has rendered a useful service in gleaning from the widely scattered medical, physiological, and biochemical literature the contributions of recent decades which relate to obesity and leanness. Everyone who desires to keep informed in these fields will find the book highly useful.

PHYSIOLOGY OF MICTURITION. *Experimental and Clinical Studies with Suggestions as to Diagnosis and Treatment.*

By Orisbello R. Langworthy, Lawrence C. Kolb and Lloyd G. Lewis. Williams & Wilkins Co., Baltimore. \$3.50. 9 x 6; viii + 232; 1940.

The original work which forms the basis of this monograph was reported in the literature by the authors and their collaborators during the period 1933 to 1940. The present systematic account of the anatomy, pharmacology, physiology and clinical neurology of the urinary bladder provides a welcome integration of their studies with those of earlier investigators in this insufficiently understood field. The book, with its 258 bibliographic citations, should prove useful to all interested in the subject.

Perhaps the most stimulating aspect of the work is the suggestion that smooth muscle, as exemplified by the urinary bladder, "has as complicated a representation in the brain and spinal cord as striated muscle, and one which appears to be similar in the principles of its actions." In support of this thesis the authors present evidence for a stretch reflex mechanism in the detrusor muscle which is under control of suprasegmental tone-maintaining and tone-inhibiting centers. These are located at the same levels of the neuraxis as are the analogous mechanisms for the control of stretch reflexes in skeletal muscle.

It would be of interest to apply the authors' views concerning the neurological control of the bladder to other smooth muscle organs. Certain experimental facts suggest that this might be particularly profitable in the case of the gastrointestinal tract. If this were done the result should constitute a sufficient comment on the present volume.



BACILLARY AND RICKETTSIAL INFECTIONS, Acute and Chronic. *A Textbook. Black Death to White Plague.*

By William H. Holmes. The Macmillan Co., New York. \$6.00. 9½ x 6½; [12] + 676; 1940.

No more adequate conception of this important book can be given than by quoting from the author's preface:

"... the mere accumulation of facts [the plan of most textbooks], however valuable they may be in actual practice, cannot be regarded as an ideal form of education." The medical student should find time "to study medicine as it has slowly evolved, and thus learn really to understand the relation of medicine to the growth of civilization." "... he would realize that there are few medical 'discoveries', but that rather our present knowledge represents the cumulative experience of many generations of priests, physicians, physicists, and philosophers, the painstaking study and observations of many centuries."

The subject matter is presented with the idea of sharpening the critical faculties of the student while acquiring habits of thinking and study; "of his becoming a man of wide interests and broad vision, and, eventually, perhaps of his becoming an educated physician." Numerous quotations are given from the writings of other men. The volume, reflecting the type of instruction now being given in courses of Internal Medicine at Northwestern Medical School, is intended to furnish sufficient material for the work of one quarter of the course in didactic medicine. It deals only with the bacillary and rickettsial infections, leaving the virus diseases, and the infections of coccal, spirochetal, and protozoal etiology for subsequent presentation.

In order to save space, no illustrations are given, but the sections are carefully documented and an excellent index has been provided.



FOODS AND NUTRITION: *A Guide for Use with the Instructional Sound Film "Foods and Nutrition."*

Prepared by Melvin Brodshaug and W. Hugh Strickler, in collaboration with A. J. Carlson and H. G. Swann. University of Chicago Press, Chicago. 15 cents. 8 x 5½; iv + 32; 1940 (paper).

ENDOCRINE GLANDS: *A Guide for Use with the Instructional Sound Film "Endocrine Glands."*

Prepared by Melvin Brodshaug and W. Hugh Strickler, in collaboration with A. J. Carlson and H. G. Swann. University of Chicago

Press, Chicago. 15 cents. 8 x 5½; iv + 32; 1940 (paper).

Each of these guides presents the script of a sound film bearing the same title. In addition, each contains a short general introduction to the subject and extensive footnotes giving definitions and more precise descriptions of certain phases of the subject not readily adaptable to sound film. *Foods and Nutrition* discusses metabolism and the effects of deficiency in each of the components of the diet. The latter is illustrated by excerpts from the film showing both man and experimental animals. *Endocrine Glands* shows briefly the method of removing portions of endocrine organs and the effect that is produced by the resulting deficiency. In turn the parathyroids, pituitary, pancreas, and thyroid are considered. Because of the brevity and simplicity of these books and films, it is doubtful that they will be of much use except for students of beginning courses.



VITAMINS: What They Are and How They Can Benefit You.

By Henry Borsook. *The Viking Press, New York.* \$2.00. 8½ x 5½; xiii + 193; 1940.

VITAMINS FOR HEALTH AND BEAUTY.

By Mabel Stegner. *Home Institute, 109 West 19th St., New York.* 15 cents. 9 x 6; 39; 1940 (paper).

Both of these treatises will be easily understood by the general reader, for whom they are written. The first is by far the more comprehensive. Borsook discusses each vitamin (or vitamin complex) separately, giving some idea of the minimum requirements for the prevention of deficiency diseases, the minimum requirements for top-notch health, some of the best food sources, a brief description of the deficiency diseases, as well as a word about buying the commercial concentrates. Five appendices deal respectively with the chief common sources of the vitamins, daily human requirements for abundant health, examples of a day's food for children and adults at different price levels, menus for children, and the vitamin contents of common foods.

The pamphlet issued by the Home Institute is understandable to anyone who can read a cook-book. The necessary facts are given concerning the function of vitamins, vitamin units found in the usual foods, sample diets, diets for growing children, etc.



PHYSIOLOGY OF THE FETUS. *Origin and Extent of Function in Prenatal Life.*

By William F. Windle. *W. B. Saunders Co., Philadelphia and London.* \$4.50. 9½ x 6½; xiii + 249; 1940.

Wilhelm Preyer's notable monograph *Specielle Physiologie des Embryo* appeared in 1887. Much of the work discussed in this earlier book has been restudied by new experimental methods, and topics which have baffled former investigators are now being solved through the ingenious technical procedures recently perfected. Windle's book is the first effort to collect and integrate the body of knowledge which has accumulated in the field of fetal physiology since Preyer's publication. The material is arranged according to organs and systems, the treatment of the fetal nervous system being particularly stimulating. The final chapter on nutrition and metabolism is brief, as this subject has been adequately covered in Needham's *Chemical Embryology*. Emphasis has been placed throughout on the strictly physiological aspects of mammalian fetal life and no attempt has been made to treat the field exhaustively. The chemistry of the fetus is dealt with "only to the point of supplying the reader with brief up-to-date synopses for the sake of completeness." However, this book should be found useful not only to physiologists and embryologists, but also to neurologists, psychologists, and pediatricians. Bibliographies are appended to each chapter and an index and illustrations have been provided.



THE ENDOCRINE FUNCTION OF IODINE.

By William T. Salter. *Harvard University Press, Cambridge; Oxford Uni-*

iversity Press, London. \$3.50. 9½ x 6; xviii + 351; 1940.

The principle underlying the use of burnt sponge by the Chinese in the treatment of goiter as far back as the thirteenth century B.C. remained obscure until the discovery of iodine in 1811. Its subsequent isolation from the thyroid in 1895 led to an understanding of the endocrine function of this element.

Salter's experiences in Harrington's laboratory in London and in Mean's laboratory in Boston have well qualified him for the task of assembling and discussing the essentials of our present knowledge of the relation of iodine to the individual endocrine organs, as well as to the complex functioning of the total endocrine system. The scope of the textual material is indicated by the chapter headings which include: Iodine stores in body tissues; Circulating iodine; Thyroid activity; Iodine and the pituitary-ovarian axis; Iodine balance; etc. Written in a completely technical and authoritative manner, the volume will undoubtedly be welcomed by clinicians, medical technicians, and endocrinologists alike.

An appendix for laboratory workers, a bibliography of 588 titles, and a complete subject index are provided.



EXPERIMENTAL INVESTIGATIONS ON THE RESPIRATORY FUNCTION IN DIVING MAMMALS AND BIRDS. *Hvalrædets Skrifter, Scientific Results of Marine Biological Research* Nr. 22.

By P. F. Scholander. Jacob Dybwad, Oslo. Kr. 12.00. 10½ x 6½; 131; 1940 (paper).

In this monograph the author reviews the literature on prolonged and deep diving of mammals and birds and adds many experiments of his own. His investigations include determinations of respiratory metabolism and of blood chemistry in seals, beavers, penguins, ducks, and porpoises, during and after submergence. The most striking results are the bradycardia in the diving mammals during diving and the increase of lactate in the blood following the dive. The author concludes from his findings that there is a

shunting of the blood from the muscles during diving and that this differential vasomotor control is an important adjustment for prolonged diving. There is a short bibliography, a section on methods, and an appendix giving complete numerical findings of the author's experiments. There is no index. The author is to be congratulated for overcoming the technical difficulties in obtaining quantitative results on the respiratory activity of the diving mammals and birds.



COMPLETE GUIDE FOR THE DEAFENED.

By A. F. Niemoeller. With a Foreword by Harold Hays. Harvest House, New York. \$3.00. 8 x 5½; 256; 1940.

HANDBOOK OF HEARING AIDS.

By A. F. Niemoeller. With a Foreword by Harold Hays. Harvest House, New York. \$3.00. 8 x 5½; 156; 1940.

The first of these books discusses, in 77 brief chapters, the structure of the ear, the various causes of deafness and other hearing defects, care of the ear, education of the hard of hearing, advice on getting the most out of conversation, lectures, movies, etc. The second describes all kinds of hearing aids, with information on the principles underlying their construction and purposes, their advantages or disadvantages, by whom they are manufactured, and, in some cases, their price. Both books are recommended as authoritative by the president of the American Association for the Hard of Hearing, Dr. Harold Hays, who contributed the introductions.

Chapter 76 of the *Complete Guide for the Deafened* consists of a list of books, excluding the medical, on hearing and deafness. Neither book is indexed.



BIRD MALARIA. *The American Journal of Hygiene Monographic Series, No. 15, July, 1940.*

By Redginal Hewitt. The Johns Hopkins Press, Baltimore. \$1.10. 9 x 5½; xvii + 228; 1940.

The many recent advances made in the

study of bird malaria are brought together in this monograph and so enables "information relative to the materials, methods and results in the entire field" to be found in one source. That such a task is valuable is obvious not only because of the intrinsic interest that the study of avian plasmodia has *per se*, but more so from the standpoint of the effect that this branch of malariology has had on the development of human malaria research. The similarity of the bird species of *Plasmodium* to that of human makes for suitable experimental techniques and controls otherwise impossible.

The geographical distribution of the parasites, host records, experimental methods and laboratory techniques, characteristics of infections, pathology, immune reactions, chemotherapy, mosquito transmission are but part of the contents. Many charts, tables, figures and a bibliography of over 500 references, make this critical review an invaluable contribution to the study of malaria.



A GUIDE TO HUMAN PARASITOLOGY For Medical Practitioners. Fourth Edition.

By D. B. Blacklock and T. Southwell.
Williams & Wilkins Co., Baltimore.

\$4.00. 9½ x 6; viii + 259; 1940.

Although written principally for the medical practitioner, this book in its previous editions (cf. Q. R. B., Vol. 14, p. 261 for mention of third edition) has found widespread acceptance among students and public health workers. The present rewriting embodies recent findings on several parasitic orders.

The authors assume that the reader has little or no previous experience in the diagnosis of parasitic diseases and start with a consideration of the necessary equipment and techniques for analysis. In turn follow concise descriptions of the various pathogenic species of protozoa, flatworms, and roundworms, including for each species the distribution, habitat, salient diagnostic characters, life histories, and clinical manifestations of the infection. These characteristics are presented in tabular form in the final chapter as are also the numerous vectors in the

spread of the organism. Such systematic descriptions facilitate the learning of a large body of data. This, coupled with a thorough index, makes for an excellent guide for the medical man or reference for the student.



LIFE AND DEATH AT LOW TEMPERATURES.

By B. J. Luyet and P. M. Gebenio. *Bio-dynamica*, Normandy, Missouri. \$4.50.

9½ x 6½; 341; 1940.

In this monograph the authors discuss the effect of low temperatures on animals and plants. The subject matter is divided into three parts: the first deals with the killing power of low temperatures, the second with the physical effects of cold on protoplasm, and the third with theories of cold injury and of death. Many references are given although the comments about these references are exceedingly uncritical. No attempt has been made to cover the practical application of these studies to food preservation or to related fields. Each part has a separate bibliography and, at the end of the book, there is a special bibliography giving the references in chronological order. There is a subject and an author index. This monograph is to be recommended to anyone wishing to find reference material on the effect of cold on biological material or to obtain a review of the theories proposed to explain cell injury and death at low temperatures.



THE AMERICAN AND HIS FOOD. A History of Food Habits in the United States.

By Richard O. Cummings. University of Chicago Press, Chicago. \$2.50. 8 x 5½; xi + 267; 1940.

A summary account is presented of the evolution of dietary habits in this country from 1789 to date. The material has been drawn from diaries, travel accounts, cook-books, newspapers and other contemporary documents. The factors which have influenced the changes in customs are many, as the author clearly points out. They include social, economic, and geo-

graphical elements as well as fads and science. The most interesting chapters are those that deal with the effects of the fluctuating medical viewpoints about nutrition on the beliefs of the people and the good use that commercial enterprises have made of the scientific endeavors. Although as a history this work constitutes only a fragmentary discussion of the subject it is well and amusingly written and is based on sound facts.



MAN, MICROBE, AND MALADY.

By John Drew. Penguin Books, Harmondsworth and New York. 25 cents. 7 x 4½; 218; 1940 (paper).

In this little book for the layman emphasis is placed on the disease-producing actions of bacteria and on common-sense precautions which can be taken to prevent infection. It is not likely that it will engender germ-phobia, as the author fears; rather, it seems to this reviewer that it will have the opposite effect, by showing that headway is being made against disease, and that there is also a great deal that individuals can do to help in the fight against epidemics. The chapter on bacterial warfare is timely.



A SURGEON EXPLAINS TO THE LAYMAN.

By M. Benmosché. Simon and Schuster, New York. \$3.00. 9½ x 6½; [8] + 317; 1940.

Believing that the layman should have available to him a non-technical account of some of the things surgeons can do, Benmosché has described the everyday operations that everyday men and women are likely to require at some time or other in their lives. The book does not contain what the doctor tells the patient as he or she is being persuaded to make the voyage from home to hospital and to operating room. It contains what the patient-to-be would like to know well in advance of the earliest symptoms of disease. The book is clearly and simply written, and it should be helpful to anyone whose fears can be dispelled by comprehension.

MORE YEARS FOR THE ASKING.

By Peter J. Steincrohn. D. Appleton-Century Co., New York and London. \$2.00. 7½ x 5; xii + 218; 1940.

The lay reader will find in these pages advice on the upkeep of his health. The case studies on the prevention of such common diseases as tuberculosis, diabetes, diseases of the blood and blood vessels, heart trouble, cancer, stomach trouble, etc. emphasize the importance of a periodic medical check-up and the intelligent cooperation between patient and physician.



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY. Vol. 47, No. 1. *Endocrine and Developmental Studies of Gonopod Differentiation in Certain Poeciliid Fishes. I. The Structure and Development of the Gonopod in Platypoecilus maculatus*, by Clifford Grobstein.

University of California Press, Berkeley. 25 cents. 10½ x 6½; 18 + 1 plate; 1940 (paper).



BIOCHEMISTRY

CHEMICAL METHODS FOR THE STUDY OF RIVER POLLUTION. *Fishery Investigations, Series I. Vol. IV, No. 2. Ministry of Agriculture and Fisheries.*

By C. H. Roberts, J. Grindley and E. H. Williams. British Library of Information, New York; H. M. Stationery Office, London. 60 cents. 10½ x 7½; 36 + 1 plate + 1 folding chart; 1940 (paper).

This monograph gives a number of procedures to enable the chemist in the field or in the laboratory to determine the concentrations of the various chemicals and chemical compounds present in polluted waters. Methods for the determination of dissolved oxygen, combined chlorine, ammoniacal nitrogen, nitrous nitrogen, free carbon dioxide, free chlorine, cyanide, hydrogen sulphide, free acids, tar bases, arsenic, iron, lead, dissolved solids, and pH value are given in detail. The tech-

niques to be used in obtaining a representative sample of the water are discussed. An appendix gives alternate procedures for the determination of ammoniacal and nitrous nitrogen by means of a Hellige comparator. A table is included for obtaining saturation concentrations of dissolved oxygen, expressed in parts by weight per 100,000 of water, at pure temperatures and concentrations of chloride. There is also included a chart for the determination of dissolved oxygen. A short bibliography and an index are appended.



DIE METHODEN DER FERMENTFORSCHUNG.
Lieferungen 2, 3, and 4.

Edited by Eugen Bamann and Karl Myrbäck. Georg Thieme, Leipzig. Lief. 2, RM. 22.80; Lief. 3, RM. 29.40; Lief. 4, RM. 30.60. 11 x 8; Lief. 2, 173-476; Lief. 3, 477-868; Lief. 4, 869-1276, 1940 (paper).

These volumes are the continuation of an extraordinarily comprehensive yet readable work (cf. Vol. 15, p. 503 for notice of the first part) by an international group of contributors who summarize the preparation and behavior of biological compounds and the modern physico-chemical techniques applicable to enzyme research.

Volume II deals with the specific preparations and behavior of the carbohydrates, nucleic acids, proteins and their degradation products, cellular reductants, and with RSH and RSSR compounds. In Volume III are discussed the methods (enzymatic, X-ray, absorption spectra, polarographic, dielectric constant, micro-melting point, etc.) used in the determination of structure. The use of nomography, redox potentials and free energies as aids to enzyme study are explained. Volume IV deals with the application of the methods described in the preceding volume in following enzyme reactions. Numerous quantitative chemical micro-methods are given. In addition, general discussions on the preparation and examination of biological materials are presented.

THE VITAMIN B₁ CONTENT OF FOODS IN TERMS OF CRYSTALLINE THIAMIN. U. S. Department of Agriculture. *Technical Bulletin No. 707.*

By Lela F. Boober and Eva R. Hartzler. Government Printing Office, Washington. 5 cents. 9½ x 6; 20; 1940 (paper).

The method chosen in the present study for assaying the thiamin content of common human foods is a comparison of weight gains in standardized B₁ fed rats with those fed a specified amount of the food in question. The literature on this and other methods is briefly reviewed. A detailed description is given of the methods of preparation of both the basic diet and of the food samples along with the statistical techniques of analysis. Approximately 100 foods are included in this report, and it is estimated that the ascribed number of units of thiamin are accurate to within 20 per cent. In view of the care with which the study was undertaken, the assays are probably well within this limit.



LABORATORY MANUAL OF BIOCHEMISTRY.

By Benjamin Harrow, Gilbert C. H. Stone, Harry Wagreich, Ernest Borek and Abraham Mazur. W. B. Saunders Co., Philadelphia and London. \$1.50. 9 x 6; v + 119; 1940 (paper).

The experiments outlined in this manual are presented with an explanatory preface to each, and illustrated directions are then given in great detail to insure a maximum of success to the student's experiment. The manual is designed for use with the senior author's *Textbook of Biochemistry* (cf. Q.R.B., Vol. 16, No. 1) or a similar text. It is bound with a reagent resistant cover. Bibliographic references and a fairly complete index are provided.



SEX

CONTROLLED FERTILITY: An Evaluation of Clinic Service.

By Regine K. Stix and Frank W. Norestein. Williams & Wilkins Co., Baltimore. \$3.00. 8½ x 5½; xiv + 201; 1940.

The group studied in detail consisted of 1497 women patients of the Birth Control Clinical Research Bureau (Margaret Sanger, Director) in New York City, between January 1, 1931 and June 30, 1932, and who were still living in the Bronx at the time they were later visited (July, 1932 to May, 1934). The report falls into four divisions: (1) a description of the group studied and a consideration of the representiveness and accuracy of the data; (2) reproductive experience (in absence of contraception, prevalence and effectiveness at attempts at contraception, and pregnancy wastage) before clinic attendance; (3) reproductive experience after clinic attendance; and (4) a consideration of some of the implications of the findings for clinic policy and management, public health and population problems. Details of methods and procedures and master tables have been put in appendices, thus freeing the text from cumbersome details not immediately necessary for an understanding of the analyses. Although the study is based on a small and atypical section of the population (but one that is gradually expanding to the proportion of a "national movement"), it is an important beginning to intensive investigations that will be necessary for an adequate assessment of the rôle of the birth control clinics in therapeutic and preventive medicine.

The bibliography covers seven pages and there is an index.



HOPOUSIA or The Sexual and Economic Foundations of a New Society.

By J. D. Unwin. With an Introduction by Aldous Huxley. Preface by Y. J. Lubbock. Oskar Pietsch, New York. \$4.00. 94 x 64; 475; 1940.

At the time of his death in June, 1936, Unwin was at work on a sequel to his *Sex and Culture* which was published in 1934. Little more than half had been put in final draft. This, together with new chapters that have been formed from those of his notes that were sufficiently

full, and some unfinished fragments, are here published under the title *Hopousia* (derived from the Greek word for *where*). In the introduction Aldous Huxley states:

[this book] treats at length of a single question: What are the conditions which must be fulfilled if a society is to go on displaying maximum energy for an indefinite period? In order to answer this question, one must, according to Unwin, discover a solution to two specific problems. First, a way must be found for making a good deal of sexual restraint indefinitely acceptable to at least the ruling classes of a society. Second, it is necessary to discover an economic system which does not, as ours so manifestly does, interfere with the display of energy, but rather fosters and encourages it. In *Hopousia*, Unwin presents his solution to these two problems.

In a series of ten appendices are given notes left by Unwin on such subjects as determinism, the influence of canon law, Hopousian economic structure, etc. A bibliography and an index are provided.



MODERN MARRIAGE A Handbook for Men. Second Edition.

By Paul Popenoe. The Macmillan Co., New York. \$2.50. 7½ x 5; xi + 299; 1940.

This second edition (first edition noticed in Q.R.B., Vol. 2, p. 144) represents a rather complete revision of the author's well-known text. While the sub-title would indicate that it is a guide for men in the art of choosing their wives and initiating a family, it is in reality a book of information for both men and women on the problems of pre-marital and marital relations. Moreover, it is far above the average of this kind of book because the advice, judgments and conclusions of the author do not in general derive from ethical considerations but in considerable amount are based on observations. For some time Popenoe has pioneered in the development of applied social biology in the field of marriage. As in all such pioneering efforts his work is not above criticism; nevertheless it represents a start which deserves to be encouraged and extended to other fields of social intercourse. An adequate list of references is included.

SEX-MORALITY TOMORROW.

By Kenneth Ingram. George Allen and Unwin, Ltd., London. 6s. net. $7\frac{1}{2} \times 4\frac{3}{4}$; 175; 1940.

The present war, the author believes, will mark "the close of a period in history, the collapse of the phase of civilization in which we have grown up" and that "any attempt to deal with the problems of sex-life must therefore take into calculation a radically altered society." His speculations as to what the new sex-morality will be do not deviate greatly from the present trend, nor do they present much that is essentially new concerning attitudes toward homosexuality, masturbation, and sex-life in schools. "The moral philosophy of the new world will certainly hesitate to suggest anything of the nature of legislation, for it will always bear in mind how varied are the characteristics, the needs, the inclinations of human beings."

**THE PHYSIOLOGY OF SEX AND ITS SOCIAL IMPLICATIONS.**

By Kenneth Walker. Penguin Books, Harmondsworth and New York. 15 cents. $7 \times 4\frac{1}{2}$; 157; 1940 (paper).

In presenting the subject of sexual relationships to the lay reader the author uses the teachings of Freud, Havelock Ellis, and Marañon for his basic tenets. The questions of sex differences, preparation for marriage, problems of sex and marriage, sex and education, and sexual deviations are covered. The section on sex and education is perhaps the best portion of the book. It should help parents to overcome their own shyness in the teaching of sex to their children. The discussion of the correlation necessary for the effective teaching of sex in school and home is adequate.

**BIOMETRY**

STATISTICAL METHODS for Medical and Biological Students.

By Gunnar Dahlberg. Interscience Publishers, Inc., New York; George Allen and Unwin, London. \$2.75. $8\frac{1}{2} \times 5\frac{1}{2}$; 232; 1940.

The arrangement of material and statistical techniques employed in this book are much the same as those found in numerous other recent texts. It differs in that it attempts to explain statistical methods and concepts in words, necessitating a modicum of mathematical knowledge. This may be a benefit to those so unfortunately limited, but the excessive use of words which could more concisely be expressed in symbols may prove irksome, if not confusing, to persons with mathematical capabilities. Although the fundamentals of probability, centering constants, variation, correlation, and skewness are adequately treated, there is little consideration of curve fitting and nothing on graphical methods or life table functions. The emphasis throughout has been on the medical aspect of statistics and almost without exception the examples have been drawn from this field. Hence the volume will find its widest acceptance by medical and public health workers. There is no list of references, but short tables of probability and an index are included.



A TREATISE ON ALGEBRA. Vol. I. Arithmetical Algebra. Reprinted from the 1842 Edition. Vol. II. On Symbolical Algebra and Its Applications to the Geometry of Position. Reprinted from the 1845 Edition.

By George Peacock. Scripta Mathematica, Yeshiva College, New York. \$6.50 for the two volumes. $8\frac{1}{2} \times 5\frac{1}{2}$; Vol. I: xvi + 399, Vol. II: x + 455; 1940.

Ordinarily, a textbook on algebra would not be reviewed in a journal such as this, but a facsimile reprint of a classic of this type should be called to the attention of scientists in general. Peacock's beautiful development of the algebraic operations profoundly influenced other students in that field, and his treatment of the subject is a delight, when contrasted with the

careless approach that we find in so many of our modern texts.

This book is strongly recommended to any biologist who considers himself a dilettante in the field of mathematics.



THE BULLETIN OF MATHEMATICAL BIOPHYSICS. Volume 3, Number 2, June, 1941.

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: Weber's theory of the Kernleiter, by Alvin M. Weinberg; The dynamics of cell constriction during division, by N. Rashevsky; A theory of steady-state activity in nerve-fiber networks: I. Definitions and preliminary lemmas, by Alston S. Householder; Studies in the mathematical biophysics of discrimination and conditioning. II. Special case: errors, trials, and number of possible responses, by H. D. Landahl; Electrical charges and potentials in cells resulting from metabolism of electrolytes, by Robert R. Williamson.



STATISTICAL METHODS. *Applied to Experiments in Agriculture and Biology. Third Edition.*

By George W. Snedecor. Iowa State College Press, Ames, Iowa. \$3.75. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; xiii + 422.

This is the second revision of this book since the first edition appeared in 1937 (1st edition noticed Q.R.B., Vol. 13, p. 376; 2nd edition, Vol. 14, p. 264. Although it follows the previous editions closely, it contains some new material in the chapters on linear regression and on large samples of enumeration data, and a completely new chapter on design and analysis of samplings. The book is of especial use to agricultural experimentalists, and presents the methods principally in terms of examples in this field.

PUNCHED CARD METHODS IN SCIENTIFIC COMPUTATION.

By W. J. Eckert. Thomas J. Watson Astronomical Computing Bureau, Columbia University, New York. \$2.00 (cloth); \$1.75 (paper). 9 $\frac{1}{2}$ x 6 $\frac{1}{2}$; ix + 136; 1940.

Although the author has selected his applications from the field of astronomy, this book will be of interest to any person concerned with the application of punched card equipment to such arithmetic operations as the construction of tables of tabular function, interpolation, mechanical quadrature, numerical harmonic analysis, and multiplication of series.



WIDTH—WEIGHT TABLES *For Boys and Girls from 1 to 17 years—For Men and Women from 18 to 41+ Years. Second Revised Edition.*

By Helen B. Pryor. Stanford University Press, Stanford University, Calif.; Oxford University Press, London. 75 cents. 11 x 8 $\frac{1}{2}$; 15; 1940 (paper).

This is the second revised edition of these well-known tables (cf. Q.R.B., Vol. 11, p. 366 for mention of 1st edition). The tables are subject, in part, to the errors that are inherent in central-value reasoning, since the regression equation is set up on an individual basis, and the tables are made up in but three broad classes of thoracic lateral width.



PSYCHOLOGY AND BEHAVIOR

THE PSYCHOLOGY OF FEAR AND COURAGE.

By Edward Glover. Penguin Books, Harmondsworth and New York. 25 cents. 7 x 4 $\frac{1}{2}$; 128; 1940 (paper).

The material in this little book was originally put together to be broadcast to the British people during the summer of 1940. The main thesis is that the morale of any country is its secret weapon, that Hitler is attempting to break this morale and that it is necessary to counter this by learning to deal with the "fifth column

in our own minds." Glover distinguishes between real fears which are to be met by vigorous preparation to meet real danger and by communal activity and close association with others, and unreal fears generated by rumor and vague suspicions. He discusses the reactions to dangers of people of various temperaments—the passive reaction in the over-anxious, the moody and depressed who feel they can't escape so why try, the aggressive who are always running into danger, the curious, the claustrophobic, etc. In the chapter, "Every man his own psychologist," he gives practical suggestions for mental first-aid in states of acute fright. For those who become overactive, from simple agitation and jumpiness to rage and violence he recommends simple sedative measures—a cigarette, weak tea or an aspirin tablet; for those who become underactive, faint or stuporous, stimulants such as coffee or a piece of candy. There is an interesting chapter on women in war-time, based on the observation that men tend to react to their country as though it were their family while women react to their family as though it were their country. In a chapter on hate and its effect on morale, Glover describes hate as an influence which blurs thinking and spoils judgment at a time when self-control is most necessary. He feels that hate is most apt to appear in an inactive population. There is danger in leaning towards another extreme too, however, and developing guilty consciences at the enemy's shouts of previous injustices, and doubts "that do some credit to our hearts but not our heads." Consciences, he states, were never meant to function at the pistol point. This matter-of-fact, simply written book is an interesting contribution to the practical and currently important problem of civilian morale.



PSYCHOTHERAPY: *Treatment that attempts to improve the condition of a human being by means of influences that are brought to bear upon his mind.*

By Lewellys F. Barker. D. Appleton-Century Co., New York and London. \$2.00. 7½ x 5; ix + 218; 1940.

In this small book Barker writes about psychotherapy and the psychobiological approach to patients primarily as they are related to the general practice of medicine. He states:

"Many physicians are so markedly repelled by the language and the ideas of some of the writers on psychotherapy (especially on psychoanalysis), that they feel that a subject so apparently recondite can be of but little value in ordinary medical practice and can be safely ignored." This attitude Barker feels is unjustified. He states: "Much of the lack of success in the treatment of patients lies in (1) failure to make a sufficiently thorough diagnostic study, or (2) failure, after comprehensive diagnostic study, to plan the therapy so as to include all the remedial agencies that are indicated by the whole situation of the patient."

Barker strongly advocates treatment of the patient as a person in every case, and in chapter V, "Methods of psychotherapy," outlines the main concepts and practices of present-day psychotherapy, not with erudite detail but in simple, practical terms. The material is descriptive rather than didactic, and offers the reader who has not specialized in psychiatry an opportunity to gain some orientation on what the psychotherapeutic field comprises. Chapter VI presents a brief discussion of psychotherapy in organic conditions. In Chapter VII there is a general survey of the types of therapeutic approach to the different functional disorders, the psychoneuroses and psychoses. Chapter VIII contains a rather oversimplified consideration of psychotherapeutic problems of the different age periods. This is not a book from which the physician trained in psychiatry will obtain special insight, but it would seem to fill the purpose for which it is intended, of indicating to other fields of medicine how psychotherapy may be a useful tool in his therapeutic armamentarium.

There is an adequate bibliography, and an index.



THE ORIENTATION OF ANIMALS. *Kinases, Taxes and Compass Reactions.*

By *Gottfried S. Fraenkel and Donald L. Gunn*. *Clarendon Press, Oxford and Oxford University Press, New York*. \$6.00. 8½ x 5½; vi + [2] + 352; 1940.

The term *orientation* is used by the authors in its broader sense to include the elementary reactions of animals to stimuli such as light, temperature, and humidity and the equilibrium of animals in relation to gravity. This is the first comprehensive account of the subject in English since Jacques Loeb's work *Forced Movements, Tropisms, and Animal Conduct* was published in 1918.

In the first part of the book Gunn has reorganized Kühn's classification (*Die Orientierung der Tiere im Raum*, published in 1919) of the various types of reaction by which animals become orientated with reference to a stimulus. The second, and more detailed, part treats the conditioning stimuli, with discussions on their type, possible modes of action, and descriptions of the set-up and manipulation of experiments, which were performed chiefly on invertebrates. Many examples and illustrations accompany the discussions. The authors have attempted in both the classification and discussion, to adhere as strictly as possible to the objective, in contradistinction to the anthropomorphic, viewpoint.

This is a highly technical work in a limited field of research but has been prepared in a readable manner. Although the reader may not agree with all the deductions and philosophical beliefs the authors have advanced as to how bedbugs, ants, worms and their ilk find their way about, he will find it a very valuable reference work. The extensive documentation and an index add to its usefulness.



A REVIEW OF THE PSYCHONEUROSES AT STOCKBRIDGE.

By *Gaylord P. Coon and Alice F. Raymond*. *Austen Riggs Foundation, Stockbridge, Mass.* \$2.00. 9 x 6; xii + 299; 1940.

This book presents a review of the clinical work of a twenty-five-year period (1910-1934) at the Austen Riggs Foundation, Stockbridge, Massachusetts. Of the 5300 cases treated during this period, a sample

of 1060 cases is analyzed, with emphasis on the method of treatment and results obtained. Both case studies and statistical approaches are used. The material is presented in three parts. In Part I, the physical set-up of the Foundation is described, the concept of psychoneurosis as a manifestation of failure to adapt to the ordinary demands of life is delineated, and the therapeutic technique of reeducation presented. Ninety-two cases are briefly reviewed and the observation made that the best results were obtained in individuals who had previously demonstrated themselves to be capable, talented and successful. In Part II, the statistical approach as a method of research in evaluating psychiatric data is discussed. Analyses of data from the Stockbridge records pertaining to sex, age at admission, marital condition, education, occupation, length of stay, number of revisits, physical disease, discharge condition and present mental condition are presented. Part III is devoted to a general summary of the entire study. There are five appendices, including six pamphlets which comprise the course of study in psychology given each patient. A brief bibliography is appended. The study is of interest as an informative presentation of the attitudes and *modus operandi* of the Stockbridge group.



THE NEUROSES IN WAR.

Edited by *Emanuel Miller*. *With a Concluding Chapter by H. Crichton-Miller*. *The Macmillan Co., New York*. \$2.50. 8 x 5½; xii + 250; 1940.

This excellent book, of multiple authorship, is a concise, practical and informative contribution to the literature of psychiatry in wartime. It presents in a matter-of-fact way a digest of the opinions and impressions of the authors, largely derived from their clinical experiences in the war of 1914-1918. Chapter I giving a survey of the literature of neuroses in war, provides a comprehensive preliminary orientation for the reader. In the succeeding chapters various prominent topics of interest are considered in more detail: mode of onset, differential diagnosis,

and treatment. Place of treatment, methods of treatment and techniques of psychotherapy are discussed and evaluated. It is notable that in only one chapter are theoretical concepts of psychopathology taken up, and here the orientation is also around the military situation and the handling is lucid. There is one chapter on psychiatric organization in the services and one chapter devoted to the problem of civilian morale. There are four appendices, a bibliography and an index. This book should be carefully read by every physician with military responsibilities.



THE HUMAN MIND. *The Key to Peace and War.*

By Alfred Hook. Watts and Co., London.

8s. 6d. net. $8\frac{1}{2} \times 5\frac{1}{2}$; x + 303; 1940.

The aim of the author in writing this book and his conclusions can perhaps best be expressed in his own words:

It has been our object to inquire into the nature of Mind as the controller of all human activity, to note the part it plays in the more important spheres of life, and to learn why it is that, in spite of the boasted intelligence and the wonderful scientific achievements of the present day, Mind has driven the world to the edge of the abyss.

We have reached the conclusion that desire, or the power to desire, is the main active principle in the mental life of man; and that it is desire that has shaped, and will shape, human destiny according to the objects to which it is directed.

For the development of his thesis the author reviews critically the thoughts of psychologists and philosophers, and presents ideas of his own, on the nature of the animal and human mind, the relations between emotion and intellect, the nature of human nature, etc. There is also a chapter on education in which the emphasis is placed on a redirection of interests of certain ambitious types so that they will be satisfied in more peaceful channels of endeavor. Neither bibliography nor index has been provided.



FROM THIRTY YEARS WITH FREUD.

By Theodor Reik. Translated by Richard Winston. Farrar and Rinehart, Inc.,

New York and Toronto. \$2.50. $8\frac{1}{2} \times 5\frac{1}{2}$; xi + 241; 1940.

This book, by one of Freud's former pupils and ardent disciples, consists of four quite unrelated parts. Part I, Freud and his followers, contains more about Freud and less of the author, and is the most interesting part of the book. Although the author writes with a breathless, reverential attitude of hero-worship towards "the master" for whom it is "our duty and our glory" to carry on, this part of the book contains observations of interest about Freud as a person. The author also offers certain dogmatic opinions about psychoanalysis which place him in a rather isolated position in relation to present-day viewpoints. For instance, he feels that a medical education is an inadequate background for the analyst (he himself is a Ph.D.) but he admits that Freud felt that he was too dogmatic on this point. Parts II and III are essentially essays commenting on various views and writings of Freud which do better speaking for themselves. Part IV consists of six essays written as birthday presents to Freud and are of sentimental rather than scientific value.



WHY MEN BEHAVE LIKE APES AND VICE VERSA or *Body and Behavior.*

By Earnest A. Hooton. Princeton University Press, Princeton, Oxford University Press, London. \$3.00. $8\frac{1}{2} \times 5\frac{1}{2}$; xxv + 234 + 10 plates; 1940.

This latest book by Professor Hooton embodies the five Vanuxem lectures which he delivered at Princeton in 1940. It consists of sketches on the distinctive traits of primates and of the principal human racial groups. From the academic viewpoint these sketches present nothing new and startling although the characteristic discursive style in which they are written and the sharp comments that accompany the factual information will appeal to the scientist as well as to the layman. The "harangue on human affairs", as the author entitles his introductory remarks which deal with the present needs of society, constitutes the most significant

part of this work even though the author is swayed somewhat by emotions in discussing the war.



THE RELATIONSHIP BETWEEN AGE AND THE STRENGTH OF HUNGER MOTIVATION. *Comparative Psychology Monographs, Volume 16, Number 4, Serial Number 83.*

By S. E. Margolin and M. E. Bunch.
The Johns Hopkins Press, Baltimore. 75 cents. 10 x 6 $\frac{1}{2}$; 34; 1940 (paper).

The investigation reported in this monograph represents an experimental attack on the problem of the relationship between age and strength of hunger motivation in white rats under certain experimental conditions. The animals were starved for varying periods. Varying intensities of electrical obstruction were then placed between them and food. Thirty-six groups, of 20 rats each, were used. It was found that there is an inverse relationship between age and maximal strength of hunger drive. Other interesting results are also reported. The study is well carried out and reported. There is a bibliography of 20 titles.



THE TERROR OF THE LEOPARD MEN.

By Juba Kennerley. Stanley Paul and Co., London. 16s. net. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; 255 + 4 plates; 1940.

Those who believe that the soul of men and animals can unite at some cryptaesthetic plane and there pass from one into the other, will find numerous observations and personal experiences in this book to substantiate their beliefs. It is all about cockatoos discovering opal mines, hares leading lost prospectors home, about werewolves and were-moose, leopard men, talking leopards, etc., that apparently abound in the wilds of various continents. Were it possible to digest the stuff without too much intestinal disturbance, the result would be a fairly good, but overlong, series of yarns.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A PHILOSOPHY OF SCIENCE.

By W. H. Werkmeister. Harper and Bros., New York and London. \$4.00. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; xii + 551; 1940.

THE PROMISE OF SCIENTIFIC HUMANISM
Toward a Unification of Scientific, Religious, Social and Economic Thoughts.

By Oliver L. Reiser. Oskar Piast, New York. \$4.00. 9 $\frac{1}{2}$ x 6; xviii + 364; 1940.

There is an oft quoted simile from the writings of Newton about a child gathering pebbles on the shore, in which the pebbles represent man's knowledge of the universe and the boundless ocean represents that which is as yet unknown.

As science advances it pushes the limits which circumscribe it back into the erstwhile domain of philosophy, but in so doing it does not curtail the activity of that faculty. Instead, it actually enlarges its scope. It has often been said that for every question science is able to answer it asks ten new ones, and speculation about the answers to these, to be intelligent, must be based upon a reasonable philosophy. In life it is often necessary to make decisions before the evidence is entirely in, so such speculation is desirable even though there be as many philosophies as philosophers.

Thoughts such as these underlie both of the present books, but in the first the problem of the synthesis of science and philosophy is attacked from different directions. Werkmeister is a philosophical scientist, and although he disclaims being a vitalist there is nothing in his work to which the orthodox vitalist is likely to take exception. On the other hand, his reiteration of the inadequacies of mechanistic philosophy is likely to excite the disapproving opposition of that school of thought. Werkmeister's personal feeling is that it is possible to steer a neutral course between Scylla and Charybdis to a third alternative, but being a scientist he makes no attempt to define this *tertium quid*. He lays the foundation for such definition, however, by expounding with clarity and in detail the revolutionary contributions to modern thought that began with the rejection by Lobatschew-

sky of Euclid's *Parallel Postulate* and which since have begun to transform even psychology and sociology. Interested readers may be grateful for Werkmeister's lucidity of expression.

Reiser is by way of contrast, rather a scientific philosopher. He advances an original doctrine to supersede both vitalism and mechanism which he calls humanism—an unfortunate name, as it has already done duty for three different systems, one of which is now pretty generally discredited, and the remaining two of which are so unlike that it is difficult for any one brought up on Aristotelian tradition to conceive of how they may be reconciled. The basis of Aristotelian logic is the law of identity, which teaches that of the two statements A is B, and A is not B, one is necessarily true and the other equally necessarily false. But Reiser's philosophy is essentially one of reconciliation, and by means of an analogy that involves modern relativity physics as well as that of the classical period he demonstrates how A can be B and be not B at the same time. Whether or not he expects in some such way to accomplish the synthesis of his own humanism with the older philosophical systems that have born the same name, he makes it clear that he believes the present time ripe for the formulation of a new logic to replace that of the Stagirite which he believes to constitute the greatest obstacle in the path of further scientific advance.

While the reviewer recognizes the importance of freeing scientific thought from the shackles of an outgrown logic, he believes that the attempt to do so by substituting another would be to jump from the frying pan into the fire. That the progress of science must be orderly and logical is obvious, but to render science subject to any logic, even a good one, would be to restrict its development.

Reiser's work is characterized by a toleration of the opinions of other writers with whom he does not see eye to eye, and it can be recommended to other philosophers as an example of how to write.

Both works are copiously indexed.

FROM THE STONE AGE TO CHRISTIANITY. *Monotheism and the Historical Process.*

By William F. Albright. The Johns Hopkins Press, Baltimore; Oxford University Press, London. \$2.50. 9 x 6; xi + 360; 1940.

In this study the author presents a chronological and geographical picture of the development of man's idea of God from prehistoric antiquity to the time of Christ, places this development in its historical context, and analyzes the historical patterns emerging from the vast amount of accumulated detail. The setting of the book is restricted to the Egypto-Mesopotamian area since "there is no focus of civilization on the earth that can begin to compete in antiquity and activity with the basin of the Eastern Mediterranean and the region immediately to the east of it."

The first two chapters are basic ones, fundamental to the reader's understanding of the author's philosophy of history and to his use of archaeological data. Chapter I treats of the history of archaeological research, the discovery and methodology of the interpretation of written documents of the ancient Near-East, unwritten documents (artifacts, uninscribed monuments etc.), and the oral and written transmission of history. Chapter II is devoted to a survey and analysis of the schools of thought on the philosophy of history. The author presents his own classification of historical stages from early and middle Palaeolithic, in the first stage, to the sixth stage *circa* 1500. The fourth stage (*circa* B.C.-700 A.D.) in this classification

reflects the author's conviction that the Graeco-Roman civilization of the time of Christ represented the closest approach to a rational unified culture that the world has yet seen and may justly be taken as the culmination of a long period of relatively steady evolution. It was in the fifth century B.C. that we find the greatest single burst of intellectual and aesthetic activity that the world has ever known, with results unparalleled before or after, from the standpoint of the integral achievement of man as intellectual, aesthetic, and physical animal. . . . It was, moreover, about the same time that the religion of Israel reached its climatic expression in Deuteronomy and Job, who represented a height beyond which pure ethical monotheism has never risen.

The following four chapters treat of the development of the idea of God and the

relation between God and man in their historical context. Chapter III is devoted to a survey of prehistory and the ancient Near East; Chapters IV and V, to Israelite monotheism and the prophetic or reformation movement; Chapter VI, to the Hellenistic Age and Jesus the Christ.

In the epilogue the author briefly recapitulates the theory of organismic philosophy in the light of the historical development of monotheism as presented in this text. Notes on the separate chapters, a key to abbreviations of journals and books, and an index are included.



CHESAPEAKE BAY COOK BOOK. *Bayfood Edition.*

By Ferdinand C. Latrobe. Illustrated by Yardley. Horn-Shafer Co., Baltimore, Md. 50 cents. 8½ x 5½; [48]; 1940 (paper).

THE EPICURE IN CHINA. *Eight Complete Chinese Epicurean Dinners.*

The Colt Press, San Francisco. \$1.50. 4½ x 6; 63; 1939.

These two booklets, both attractively illustrated, furnish many interesting and dependable recipes. The first, dealing with familiar sea food now readily procurable in most parts of the United States will appeal to a wider group than the second.

The place of honor in the *Chesapeake Bay Cook Book* is given to terrapin and turtles, with only four ways of preparing them. But the oyster, crab and many fishes are represented by numerous excellent recipes, only to be tried to be found very palatable. Lobster, scallops, and shrimps are included because they are always in the Maryland markets and are used extensively. Although most of these recipes have been in use for generations in the Chesapeake region their origin in many cases is unknown.

That Chinese food is being increasingly used in this country is evident by the fact that it is now possible to obtain so many of the ingredients in tins. In *The Epicure in China* we find several of our favorite dishes and many that we hope to try. We were unaware, however, that corn-starch [our abomination] is so widely used in the preparation of Chinese food.

CHAMBERS'S TECHNICAL DICTIONARY. *Comprising terms used in Pure and Applied Science: Medicine: the chief Manufacturing Industries: Engineering: Construction: the Mechanic Trades. With Definitions by recognised Authorities.*

Edited by C. F. Tweney and L. E. C. Hughes. The Macmillan Co., New York. \$5.00. 8 x 5½; vi + 957; 1940.

This dictionary containing many thousands of technical terms and abbreviations, covering the subjects (from acoustics to zoology) under the broad headings indicated in the sub-title, will be found extremely useful by scientists, manufacturers, technicians, editors, teachers, students, and the technically-minded general reader. In addition to the strictly technical terms which do not ordinarily form a part of every-day speech, many common terms such as *accuracy*, *apple*, *capitalist*, and *speed*, which have acquired special meanings in one or another branch of science, have been included. All the definitions, many of which have been formulated for the first time, are by specialists in their respective subjects. Tables of chemical terms, periodic systems, igneous rocks, sedimentary rocks, the vegetable and animal kingdoms, and a bibliography arranged by subject, are appended.



SCIENCE IN PROGRESS. *Second Series.*

By L. J. Stadler, F. W. Went, J. F. Fulston, Douglas Johnson, Alfred C. Lane, H. P. Robertson, Carl D. Anderson, Duncan A. MacInnes, J. W. Beams, and J. C. Hunsaker. Edited by George A. Baitsell. Yale University Press, New Haven; Oxford University Press, London. \$4.00. 9½ x 6; xii + 317; 1940.

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THE QUARTERLY REVIEW *of* BIOLOGY



THE MORPHOLOGY AND DEVELOPMENT OF THE WING PATTERN OF LEPIDOPTERA

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INTRODUCTION

THE surface pattern of animals involves important questions for several branches of biology. Taxonomists often use pattern features for distinguishing between species. Some pattern formations have a definite ecological value, and the imitation patterns, e.g., the leaf imitations by the wings of different kinds of butterflies, have played an important rôle in the discussions about natural selection. On the other hand, the developmental implications of pattern formation have a bearing on many problems of general developmental physiology. Goldschmidt called attention to the fact that all developmental processes may be regarded as pattern formations, i.e. the creation of differences in a previously uniform material. The wing pattern of Lepidoptera seemed to him an extremely convenient material for the analysis of developmental questions, since it is two-dimensional only and develops in relatively late stages of life. Also, since it is of only minor importance for the life of the organism, operations can be easily executed.

In the actual analysis of the wing pattern of Lepidoptera investigators have tried to follow all these suggestions. The analysis has succeeded in a singular way in combining the methods of comparative morphology, of genetics, and of experimental embryology. In this way a certain part of the pattern problem in Lepidoptera has already been solved, giving major contributions to problems of general importance, such as the action of genes, the resemblance between gene effect and modification and the determination process.

DESCRIPTION OF PATTERNS

*The pattern of *Philosamia cynthia**

The first task of pattern analysis consisted in giving an adequate description. The first important step was made when Schwanwitsch (1924) and Sueffert (1925, 1927) showed that the wing pattern of butterflies and moths must not be regarded as a whole, but must be divided into several independent *systems*.

Pattern elements are regarded as belonging to the same system, when, from one species to another, they are found to vary

concomitantly and independently of other pattern elements. The same concomitant variation of pattern elements belonging to the same system is found in individual fluctuations within a single species, as Henke (1928) has shown in a population of *Larentia sordidata* (Geometridae.)

In many species two transverse bands are found crossing the wing. Each band may be composed of one color only, or of

round has a somewhat darker coloration than the two fields bordering the bands at the outside and at the base of the wing, and it is therefore designated as the "central field" (discal area) in distinction from the "outer-fields," which embrace the "external field" (post-discal area) distally and the "internal field" (basal area) proximally. Both outer-fields have the same coloration. The central field

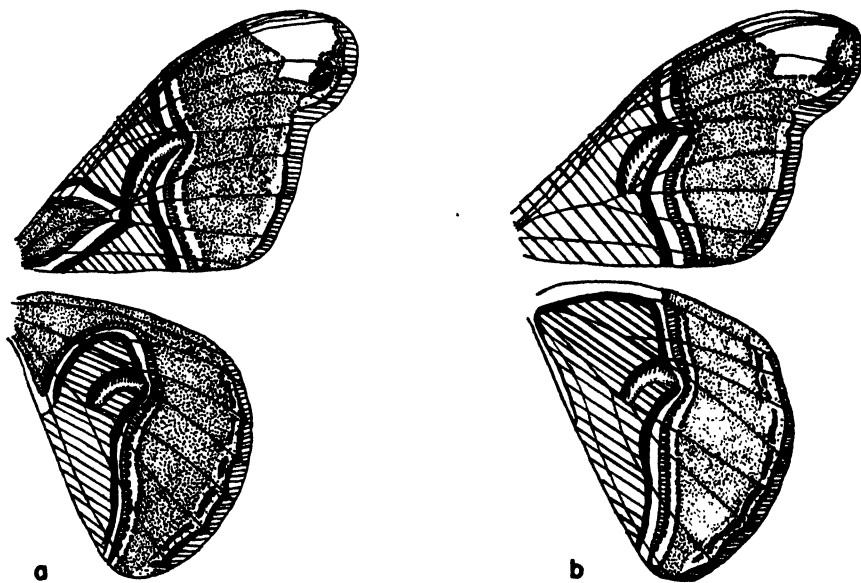


FIG. 1. SCHEME OF THE WING PATTERN OF *PHILOSAMIA CYNTHIA*
(a) upper side; (b) under side. Simplified after Henke (1936)

two or even three differently colored stripes, as in the case of the Ailanthus silk-moth, *Philosamia cynthia* (Fig. 1), which has been analyzed by Henke (1933). In this species, the three colors of the band are black, white, and pink, and it appears clearly that the colors in the two bands are symmetrically arranged about the field which lies between the bands: in each case black is the innermost stripe, pink the outermost one. Therefore, the bands have been called "symmetrical bands" (Sueffert). The area they sur-

round and the bordering bands together are called the "symmetrical system."

Another element, almost constantly found in Saturnids and often among other Lepidoptera is characterized by its situation on the transverse discal vein, the discocellulus, or when this vein is lacking in the adult moth, as in *P. cynthia*, between the cubital and medial vein systems (Henke 1933). In Saturnids it often forms an ocellus, consisting of differently colored bands. In *P. cynthia* it is extended forming a crescentic spot, which, how-

ever, still shows the differentiation into different bands characteristic of the typical ocellus. Its center lacks scales almost completely, and the bare epithelium has a glasslike appearance. The center is surrounded by a white line which is followed by a yellow one. Following closely the shape of the ocellus outside of the yellow stripe, a black line is found at the fore edge of the ocellus only, and is in direct connection with the black stripe of the symmetrical bands.

Whereas the internal field of *P. cynthia* is homogeneous, the external field shows several differentiations. Closely attached to the external zone of the distal symmetrical band a long area appears, not well defined against the external field but distinguished from it by its lighter color—the so-called "external shadow."

Near the tip of the wing a lilac area is found, the "apical patch," which is bordered distally by a clear-cut white line, the "apical line." An ocellus, dark in Fig. 1, which is lying on its inferior margin, seems to belong to the same system, but comparison with other species reveals its complex origin. Only the innermost white stripe is a continuation of the apical line. The outer dark part belongs to the outer-field, whose boundary against the marginal elements may be marked by a band of dark scales.

In the marginal area of the wing, the borderline, running parallel to the wing margin, divides the distal "marginal field" from the more proximal "border-field," which again is clearly distinguished from the external field by its lighter coloration. This boundary of the border-field against the external field is marked in many species by a distinct band, whose topmost part is encountered in *P. cynthia*, forming the above-mentioned part of the apical ocellus.

The general type of wing pattern of the family Saturniidae

In the same way, the wing pattern of many Lepidoptera has been described. If only a certain group of related species is considered, comparable elements in different species are found. By comparing a large number of species and proceeding from group to group, it has been possible to develop schemes containing all pattern elements occurring in a certain family, i.e. a *general type* for the wing pattern of this family. Schwanwitsch and Sueffert first suggested independently a type for the wing pattern of Nymphalids, and the striking similarity of those two

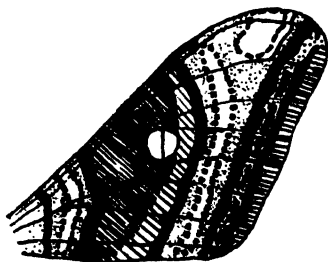


FIG. 2. GENERAL TYPE OF THE WING PATTERN OF SATURNIDS
After Henke (1935)

attempts forms strong evidence for the reliability of the method. Henke proposed a scheme for the wing pattern of Saturnids which will be more extensively described as the physiological analysis in Saturnids has proceeded comparatively far (Fig. 2).

Many of the elements found in this scheme have already been encountered in *P. cynthia*. The two dark bands across the wing represent the symmetrical bands, including the hatched central field. Inside the central field, the colorless ocellus and a heavily hatched band, the central shadow, are indicated in the figure. The part of the central field proximal to the central shadow has been represented by

another kind of hatching, indicating that this field in some species is distinguished in coloration from the distal part of the central field. The outer-fields on both sides of the central field, the external field and the internal field, are dotted in the same way in the drawing, in order to show that they are colored alike. The external field may contain an external shadow (colorless in the drawing), and the internal field sometimes exhibits a corresponding internal shadow. At the tip of the wing the apical patch is represented by a colorless area, bordered at the distal side by the apical line. The boundary of the external outer-field against the border elements may be marked by a line or band. The internal field may be separated in a similar way from a basal field. The two fields close to the margin of the wing, the proximal border field and the distal marginal field, are divided by a line. The border field may contain a row of spots, the so-called "pseudo-submarginal spots" (heavily stippled in the sketch) which are found, e.g., in the hind-wing of *P. Cynthia* (see Fig. 1).

It must be emphasized that several elements of minor importance have been omitted in this sketch, namely several fields which never form border elements but only cause minor variations of coloration in the areas they cover, some rhythmical pattern elements, and some elements dependent on the structure of the wing, e.g., a distinguishing coloration of the veins.

Starting from this scheme every wing pattern occurring among Saturnids can be derived. In all special cases only a part of the possible elements is developed, while others are lacking. Furthermore, the elements which occur may be differently developed and differently colored in different species.

A band may consist of one color only,

or of two or even three differently colored stripes. It may be constricted at the level of a vein or even dissolved into a row of spots. A band may be interrupted at the level of a vein, while the other part of the band is displaced and continues for a certain distance proximally or distally from the same vein, a phenomenon to which Sueffert has applied the geological term "dislocation." A special case of dislocation is the so-called "pierrellisation," first described by Schwanwitsch in the genus *Pierella*. In this case, parts of different bands are displaced in such a way that they form new lines which seem a

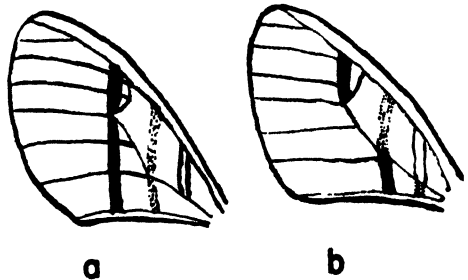


FIG. 3. PIERELLISATION OF TRANSVERSE BANDS IN THE GENUS *PIERELLA*

(a) typical pattern; (b) formation of combined bands by means of dislocations. From Henke (1935) after Schwanwitsch.

unit at first sight but which are in fact composed of parts of morphologically different bands (Fig. 3).

Pierellisation, on the other hand, illustrates the fact that parts of different morphological origin can combine into an optically uniform entity, as has already been shown for the apical ocellus in *P. Cynthia*. The occurrence of this phenomenon is a special case of the principle, first investigated by Henke (1936), that pattern elements often prefer a certain position on the wing, and that at such places several elements of different morphological value may be encountered very close and parallel to each other, like

the external shadow of *P. cynthia* which lies exactly parallel to the symmetrical band. In other cases, two different pattern elements may even cover each other so that they cannot be distinguished. In normal *P. cynthia* specimens, for example, no internal shadow can be found. However, in abnormal specimens, in which the central field is reduced in size and the symmetrical bands are nearer each other than in the normal case, a clear internal shadow at the ordinary place of the proximal symmetrical band is seen. This suggests that it is ordinarily present

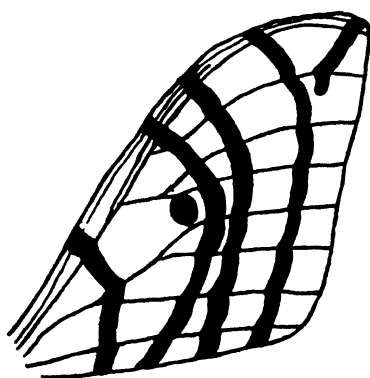


FIG. 4. MAIN PATTERN LOCI FOR THE WING PATTERN OF SATURNIDS
After Henke (1936)

but covered by the proximal band (Henke, 1936). Quite a few instances of close parallelism or even partial or complete overlapping of different pattern elements suggested the conclusion that certain areas of the wing, *pattern loci* (Henke), are most likely to contain pattern elements. Fig. 4 shows the chief pattern loci of the Saturnid wing.

The wing of P. cynthia considered as a tridimensional object

The upper side of the hind-wing and the under side of both wings show pattern elements similar to those on the

upper side of the fore-wing. A close examination of those patterns in *P. cynthia* led to new points of view (Henke 1933b). The upper side of the hind-wing possesses a symmetrical system like that of the fore-wing, with the difference that the proximal and distal symmetrical bands unite anteriorly (see Fig. 1). In this way the central field does not reach the foremost edge of the wing, but is open towards the hind border of the wing only. The same is true for the under side of the hind-wing, so that the central fields of upper side and under side are in connection at the hind edge of the wing only. It seems justifiable to consider the central field of upper side and under side as one continuous field, bending around the hind margin of the wing and covering it in the manner of a clamp. The whole system would be surrounded entirely by the symmetrical band. A difficulty of this view appears in the fact that the proximal band of the under side reaches the hind margin somewhat nearer the base than the corresponding band at the upper side. Close inspection of the hind margin of the wing, however, reveals that both bands are connected by a narrow line of white scales following exactly the hind margin of the wing. If it is kept in mind that the wing actually is a tridimensional object, consisting of a bag of epithelium evaginated from the body surface, it is clear that a part of this epithelium, the central field, which covers part of the upper surface as well as the under side of the wing is entirely surrounded by a line and distinguished in coloration from the surrounding outer-field.

This conception can also be applied to the fore-wing of *P. cynthia*. The under side in this case shows only the distal symmetrical band and the central field reaches the base of the wing. The proximal band of the upper side bends at the

fore and hind edge towards the base, but does not reach it. A connecting line which closes the central field, such as is present on the hind wing, cannot be found. However, even this fact fits the conception of a continuous central field on upper and under side, surrounded by the symmetrical band, if the phenomenon of dislocation is taken into consideration. It means in this case that parts of a band may be shifted against each other at the margin of the wing as well as at certain veins in other cases. This view is con-

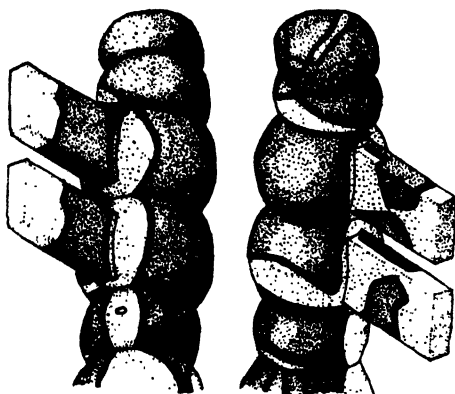


FIG. 5. TRIDIMENSIONAL SCHEME OF THE ARRANGEMENT OF CENTRAL FIELDS AND OUTER-FIELDS ON THE WINGS AND BODY OF *PHILOSAMIA CYNTHIA*

Central fields, dark; outer-fields, light; symmetrical bands, black. After Henke (1933b).

firmed by the observation that under experimental conditions a proximal band may appear at the under side of the fore-wing. Following this conception, the central field of the fore-wing constitutes a large band wound around the whole wing, having a constriction in the middle of the upper side. Under certain conditions it can be divided at the level of this constriction in such a way that an incompletely closed band appears around the whole wing. In this case two independent central fields seem to be present at the upper side, both surrounded by a sym-

metrical band and open against one of the edges of the wing. In Fig. 5, a tridimensional scheme for the wing pattern of *P. cynthia* is given, the wings being represented by squares in which the situation of the central fields is marked. On the fore-wing, the abnormal case of a divided central field has been supposed. The central field as it is regarded here, lying on upper and under side of the wing and entirely closed from the outer-fields by the symmetrical bands, shows a concentric arrangement and therefore it has been proposed (Sueffert, 1929; Henke, 1933a) to include it together with the discal ocelli, whose concentric arrangement is obvious, under the name "centric systems."

The wing pattern as part of the body pattern

It is clear from this explanation that the whole wing of *P. cynthia* and other Saturnids is divided into two kinds of areas, a continuous central field and two bordering outer-fields. It has been shown (Henke, 1933b) that a similar division in central fields and outer-fields can be found in the body pattern which is well developed in the subfamily Attacini to which *P. cynthia* belongs. The distribution of central fields and outer-fields on the thorax and the first two abdominal segments of *P. cynthia* has been represented schematically in Fig. 5, dark shade meaning central fields and light shade the outer-fields. Actually, the decision whether a bordered field of the body of *cynthia* is a central field or an outer-field is not easily made, since the color differences between the two kinds of fields are very slight. Therefore, the differences of coloration in the different zones of the bordering bands are used as a criterion, black being adjacent to the central field and red to the outer-fields. This difference is well developed in certain moths belonging to the

genus *Rothschildia*. By comparison with those species, the decision whether a certain field of the body is to be considered as a central field or as an outer-field is reliably possible even in species like *P. cythia*, which does not show this color difference between the zones of the borderlines in the body pattern.

In this way, the arrangement of the wing into central field and outer-fields has to be considered as a special case of the differentiation of the whole body surface, of which the wing epithelium is a part. The whole body surface is divided into two kinds of areas, central fields and outer-fields, and the same differentiation is found in the wing. The richer pattern of the wing arises from the interaction of the other pattern systems indicated in Fig. 2.

The field character of pattern elements

The other elements occurring in the Saturniid wing can also be regarded as fields or as field border differentiations, as has already been shown for the symmetrical system, the symmetrical bands in this case being field border differentiations. In order to describe all occurring cases in terms of this conception, Henke (1936) has distinguished three types of boundary formation. In type I the two fields have different coloration and meet each other without border differentiations, e.g., external outer-field and border-field in *P. cythia*. In the second type, the two fields have also different colors, and are divided by borderlines. The symmetrical system and the outer-fields of *P. cythia* are an example of this type. In type III the borderlines divide two areas of the same coloration, so that the border differentiations seem to emerge from a uniform background. However, in an example of this type, the symmetrical system and the outer-fields of the meal moth, *Ephestia kuehniella*, differences be-

tween the equally pigmented areas appear under the influence of certain genes (Whiting, 1919; Kuehn, 1937, 1939b) and of external modifying factors (Strohl and Koehler, 1934). (See below.)

Adaptive patterns

By means of the methods described a great many patterns of Lepidoptera have been analyzed, and it has been possible to reduce even very complicated ones to special cases of the general type. Special interest is found in adaptive patterns, e.g., patterns which cause the wings as a whole to resemble a leaf. Sueffert has succeeded in describing the complicated pattern of the leaf-butterfly *Kallima* in terms of the Nymphalid scheme, and Henke (1936) similarly analyzed a number of adaptive patterns in Saturniid moths. The resemblance to a leaf in all those cases is effected chiefly by a dark line crossing the wing obliquely, giving the impression of the mid-vein of a leaf. However, this line may correspond in different species to different pattern elements, e.g., distal symmetrical band, central shadow, or border of the external outer-field. Or it may even be composed of different parts of different morphological value, as distal band plus border of the external field (*Solus drepanoides*); or distal symmetrical band plus proximal band of the ocellar system (*Kallima*, Nymphalidae). The latter cases provide an instance of the phenomenon called "total pattern" by Sueffert (1925)—the collaboration of independent elements of different origin in the production of an optically uniform effect. In the case of the leaf-imitating moths it may be explained by the existence of a pattern locus that crosses the wing obliquely and which can be occupied by different elements. The problem is, however, complicated by the collaboration in some species of the hind-wing in the

production of a leaf-imitating impression. In those cases, the hind-wing too is crossed by an oblique line, corresponding to the line on the fore-wing in coloration and continuing it exactly in the normal wing position, contributing to the effect that fore- and hind-wing together look like a leaf. An explanation of the fact that two lines of different morphological value on different wings may be arranged so as to give a uniform optical effect, is not yet possible.

The pattern systems, developed by a purely morphological analysis, are considered as homologies by Schwanwitsch, and he has followed their variation from species to species and from group to group among the Nymphalids, using it as evidence for the evolutionary connection between different species. Henke, although not denying the possible importance of the study of patterns from this point of view, considers it especially as yielding evidence for comparable processes in ontogeny, and uses for this conception the term "plastology." Two formations are called plastologous, if they are originated by equivalent developmental processes. The symmetrical bands of different kinds of Lepidoptera, for example, are regarded as plastologous, implying that they are caused in the same way. In this way, the morphological findings furnish a starting point for the experimental analysis of the origin and development of wing patterns which has already proceeded considerably through the work of Kuehn, Henke and their collaborators.

The chief experimental animal for this work hitherto has been, besides *Phlosamia cynthia*, the meal-moth *Ephestia kuehniella*. Its very simple pattern will be described briefly (Fig. 6). The symmetrical bands consist of three zones, of which the middle one is white, the other

two being dark. The central field enclosed by the bands has the same greyish or brownish coloration as the outer-fields. Inside the central field, two kinds of elements are encountered, the central shadow and the discal element. The former is present in most of the strains in the form of four dark spots, the shadow spots. The discal element is represented by two dark "central spots" and a white spot between them. At the margin of the wing, 5 dark marginal spots are found lying between the veins.



FIG. 6. WING-PATTERN OF THE FLOUR-MOTH *EPHESTIA KUEHNIELLA*

After Kuehn and Henke (1929)

ONTOGENETIC PROCESSES CONCERNED IN PATTERN FORMATION

The reaction of pattern systems on environmental factors

Pattern elements belonging to the same system have been shown to react in the same direction under modifying influences. After treatment by high or low temperature at a certain time after pupation, the "sensitive period," changes in the pattern of Lepidoptera may be obtained. That every morphological system has its own distinct sensitive period was first proved by Kuehn (1926) in *Argynnis paphia*. Later on the sensitive periods of the different systems in *Ephestia* were thoroughly examined by Feldotto (1933), by Kuehn and Henke (1936), by Wulkopf (1936), and by Stubbe (1938). Feldotto, testing the effects of heat shocks, i.e. brief exposures to barely sub-lethal high temperatures (47°C.), found that at different times after pupation elements belonging to different systems react in a different way.

Elements, however, which belong to one and the same morphological system always showed deviations in the same direction (Fig. 7). After a heat shock shortly after pupation, the marginal spots increase in size, i.e. the number of dark scales forming the spot is increased. A maximum number of dark scales in the marginal spots is obtained after heat treatment at 36-48 hours after pupation. Heat treatment of somewhat older pupae has a smaller effect on the marginal spots, and following a heat shock applied 72 hours after pupation the marginal spots become even smaller than in untreated specimens. After this time, a heat shock has no effect at all on the marginal spots.

On the other hand, the dark elements of the symmetrical bands show an entirely different kind of reaction to heat. Heat treatment shortly after pupation diminishes the intensity of the dark bands, reaching a minimum at 24-36 hours after pupation. Shortly after this time, a heat shock does not influence the intensity of the bands as compared with untreated animals. But later on, at a time when heat treatment no longer affects the marginal spots, the intensity of the symmetrical bands attains a second minimum after a heat shock. After this time, the curve for the intensity of the black bands after heat treatment returns gradually in the direction to normal.

Another sensitive period has been found for the size of the central field. Following heat treatment shortly after pupation, the symmetrical bands are removed from each other, so that the central field is extended. Later on, heat treatment causes the bands to approach each other, reducing the size of the central field considerably. The maximum reduction is found following a heat shock applied 48-60 hours after pupation.

The results of Feldotto were confirmed

and enlarged by Wulkopf and by Stubbe. They also established sensitive periods and characteristic reaction curves for the central shadow and the central spots. Characteristic alteration curves for the

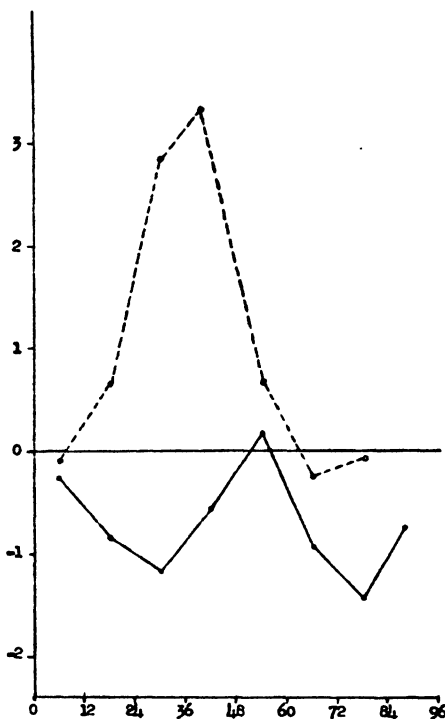


FIG. 7. SENSITIVE PERIODS OF THE INTENSITY OF THE SYMMETRICAL BANDS (—) AND OF THE NUMBER OF SCALES IN THE THIRD MARGINAL SPOT (---) OF *EPHESTIA KUEHNIELLA*

Abscissa: age of the pupae at the time of heat treatment, in hours after pupation. Ordinate: mean of the animals treated at the respective times, expressed in standard deviations for the variation of the controls. 0: mean of the controls. Positive values indicate increase, negative values decrease as compared with the controls. From Kuehn and Henke (1936) after Feldotto.

different systems were also found after a short treatment with low temperature and after a prolonged exposure to moderately high temperatures (35°C.). The effects of these influences were in some systems equal to those produced by a short

heat shock of 47°C., in other cases, however, they were different.

Comparable results have been found in experiments with *Argynnis paphia* (Kuehn, 1926), *Vanessa urticae* and *io* (Koehler and Feldorto, 1935), and *Abraxas grossulariata* (Kuehn and von Engelhardt, 1936). Therefore the fact that elements belonging to the same morphological system have the same sensitive period, seems generally well established for Lepidoptera. This fact holds true for all species studied, although the relative time of the sensitive periods and the manner of reaction of plastologous systems may be different in different species.

The developmental independence of different systems in *P. cynthia* has been shown by means of operations on the imaginal wing buds in late caterpillars and on the pupal wing (Henke, 1933a). The symmetrical system and the ocellus have been shown to be independent from each other in respect of size, position on the wing, and coloration. The ocellus could be diminished in size without a corresponding change in the central field, and vice versa. The ocellus, which lies in normal cases inside the central field, could become partly or even entirely removed from it into the external field. An operation in the early pupa affects the coloration of the symmetrical system; red scales are scattered in the symmetrical bands and in the central field, but not in the outer-field nor in the ocellus. The white zone of the symmetrical band may appear pinkish on account of the interspersed red scales, whereas the white zone of the ocellus keeps its pure white color. The outermost black stripe of the ocellus, however, behaves in this experiment like the black stripe of the symmetrical band. Therefore it must be concluded that, although its shape and position are

determined by the ocellus, its coloration follows that of the symmetrical band.

Also in other cases, experiments have revealed differences between elements which in the morphological analysis first seemed to be parts of the same system. In *Abraxas* the symmetrical bands consist of three zones, a yellow line in the center bordered against the central field and against the outer-fields by a row of black spots. In the experiments of Kuehn and von Engelhardt (1936), involving alterations of temperature in the pupal stage, the outermost row of black spots showed an entirely different sensitive period from the innermost one. A similar fact has been recorded in *Ephestia* by Stubbe. The innermost dark stripe of the symmetrical bands shows a stronger reaction to a prolonged influence of a moderately high temperature than the outermost dark zone. The latter, however, reacts much more strongly to a short heat shock. In both cases, the behavior of the outermost dark stripe of the symmetrical bands resembles more that of the marginal spots than that of the innermost zone of the band. This behavior indicates that the outermost zone of the symmetrical bands does not belong originally to the symmetrical system, an assumption that will be shown below to have been proved by other experiments.

The reaction of pattern systems on genetic factors

The different systems show their developmental independence also under the influence of Mendelian factors. A number of genes have been described in *Ephestia* which act on the size of the elements of one system only. There are genes influencing the intensity of the symmetrical bands (one of them sex-linked (Kuehn and Henke, 1929, 1932; Huegel, 1933; Clausen, 1937; Schwartz, 1938)), of the marginal spots (Kuehn and

Henke, 1929), of the central shadow (Clausen, 1937), and of the central spots (Kuehn and Henke, 1932) which affect the number of dark scales in the respective systems exclusively.

Other genes have a certain influence on the arrangement of scales in a certain system without affecting its size. The gene *rb* (Clausen, 1937) affects the shape of all marginal spots. They are broader and narrower in *rb**rb* animals than in *Rb*-animals, so that they even may join each other forming an uninterrupted band at the margin of the wing. Two genes influencing the size of the central field and the position of the symmetrical bands have been found by Kuehn and Henke (1936). The dominant gene *Sy* (lethal when homozygous) causes the bordering bands to approach each other, diminishing in this way the size of the central field. Another factor *Syb* (intermediate in the heterozygote) enlarges the central field, removing the bordering bands from each other. The effects of those genes resemble the effects of heat shocks applied in the sensitive period for the size of the central field in normal animals. The effects of temperature treatment in these sensitive periods are therefore to be considered as phenocopies of the genes in question—using a term proposed by Goldschmidt. The meaning of this phenomenon in this case can be analyzed by simultaneous influence of the temperature and the genes. The experiments have shown that the actions of both these genes and of temperature treatments during the sensitive period of the corresponding regions are additive. The central field of a *Sy*-wing is enlarged in the direction to normal by a heat shock in the early part of the sensitive period, as well as by the presence of the gene *Syb* in the same animal. It is still further reduced by the influence of heat in the later part of the sensitive

period. It is, however, impossible to enlarge the central field of a *Syb*-wing by an additional heat treatment in the early part of the sensitive period. The possibility of combining the gene effects with the modificatory influences suggests that both act on the same developmental process.

A sex-linked gene *dz*, described by Kuehn (1939b), has an influence on the central field which is similar to the gene *Sy*, but sometimes its effect is even stronger. For in *dz dz*-animals, the central field may be reduced in size to such a degree, that the white distal and proximal bands join in the middle of the wing, dividing the central field in an anterior and posterior part. The gene *dz*, besides influencing the size of the central field, also affects its pigmentation, the central field of *dz dz*-animals appearing sooty.

By the whole bulk of evidence, it becomes clear that the conception of pattern systems is not merely a generalization from morphological observations, but that every system constitutes a unit of its own for genetical and environmental influences. A system appears as a number of pattern elements which are determined by the same ontogenetic process. Further analysis described below will give some evidence concerning the nature of this determinative process.

It must, however, be emphasized that the independence of the different systems and the uniformity of reaction of elements belonging to the same system is not absolute. Several genes have been described in *Ephesia* which influence two systems at once. A gene found by Huegel (1933) affects at the same time the intensity of the white symmetrical bands and of the white parts belonging to the central spots. The above mentioned genes *Sy* and *Syb*, besides influencing the size of the central field, affect the situation of the central

spots on the wing (Kuehn and Henke, 1936). Schwartz (1938) described three genes which act on the expression of single bands belonging to the central system, namely the proximal internal band, the distal internal band, and the distal external band, respectively. On the other hand, Koehler and Feldotto (1935) found in *Vanessa urticae* that the sensitive periods of relatively remote parts of the same system are slightly different.

*The determination of the central system in
Ephestia*

An analysis of the process determining the shape and size of a system has been successfully started in the case of the central system. Kuehn and von Engelhardt (1933) made slight burns on the pupal wing of *Ephestia* with the aid of a microthermocautery. Three types of reaction could be sharply distinguished, depending on the time of operation. In the first period, during the first day after pupation, the effects on the wing pattern were entirely local (Fig. 8). The white zone of the symmetrical band was bent around the operation scar, so that the scar always lay in the outer-field. The external dark symmetrical band is always situated at the external side of the scar, divided by it from the white line. The other parts of the wing remote from the scar are not changed. If the defect has been set in the region of the anal vein—a vein which is found in *Ephestia* in the pupal wing, but not developed in the adult moth (Behrends, 1935)—the symmetrical field becomes divided into two parts, each bordered by a band and open to the anterior or posterior margin of the wing, resembling the cases in *P. cynthia*, which are schematically represented in Fig. 5, as well as some pictures obtained after heat treatment at the maximum of the

sensitive period for reduction of the central field, or under the influence of the gene *dz* in *Ephestia*.

If a great number of operated wings, containing cautery marks at different points, are compared, the pictures obtained for the central system suggest a determination stream which is spreading over the wing after the time of operation and cannot pass over the scars. The border of this stream would be constituted by the white band, while the outermost dark zones lie outside of the scar and belong obviously to the outer-fields, a fact already suggested by their behavior in the temperature experiments. The course of the determination stream can be reconstructed from the pictures obtained by operating at different points. It seems to enter the upper side of the wing from the fore as well as from the hind edge. Both currents spread over the wing and meet in the anal vein region, spreading afterwards in proximal and in distal direction until they reach the usual situation of the white lines, if they are not held back by an area of cells which have been killed by the cauterization (Fig. 8k).

In the second period, 48–60 hours after pupation, an entirely different type of reaction is encountered. After an operation at this time, the whole central field is reduced in size, regardless of the situation of the defect. Different grades of this reaction are found and indicated schematically in Fig. 8—low grades of reduction, resembling the action of heat treatment in the second part of the sensitive period for the size of the central field or by the gene *Sy* or *dz*, and higher grades, in which the central field may even be divided into two parts at the level of the anal vein. If the central field is considerably reduced in size by the operation, the different parts constituting the symmetrical system are not all reduced to the

same extent, but the white and even the extreme reduction even the dark zone may be missing, the symmetrical system

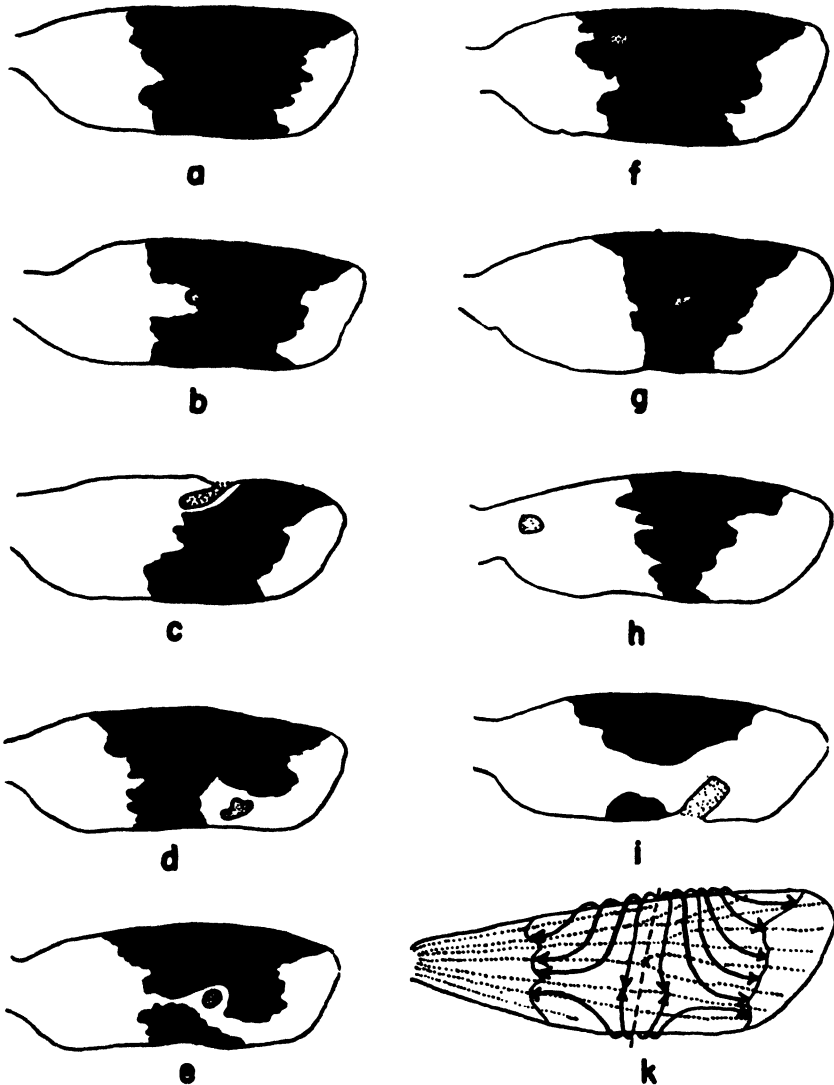


FIG. 8. ALTERATIONS OF THE SYMMETRICAL SYSTEM OF *EPHESTIA KUEHNIELLA* AFTER CAUTERIZATION

(a) normal. (b-e) after cauterization at the first day after pupation (local reaction). (f-i) after cauterization at the second and third day after pupation (general inhibition of the spreading process). Symmetrical system, black; outer-fields, white. Schematically from Henke (1935) after Kuehn and von Engelhardt. (k) scheme of the spreading process. After Kuehn and von Engelhardt (1933).

than usual. In those cases the ground color may be reduced even to the point of complete disappearance. In cases of being represented by white scales only. This particular behavior—that in the reduction of a centric system (symmetrical

system, discal ocellus) the innermost parts disappear entirely before the outer parts are reduced—has been found in many instances and has been called "pauperization rule" by Henke (1933a).

The pictures of progressive reduction of the central field can easily be arranged into a series, which suggests also a determination stream spreading over the wing surface, exactly fitting the picture constructed from the results obtained by operations in the first period. The results lead to the idea that the time, during which the second type of reaction is found, is exactly the time of spreading of the determination stream over the wing, and that this process is suddenly stopped by the operation, the final result indicating the situation of the determination stream in this particular moment. This conclusion is confirmed by the fact that the time in which this type of reaction is found after cauterization is exactly the sensitive period during which a reduction in size of the central field may be obtained by heat treatment.

After the time of spreading of this stream over the wing surface, the determination of the central field is completed. Later cauterizations led to a third type of reaction, consisting in a destruction of the scales in the burned area only, without any influence on the pattern.

The action of the genes Sy and Syb on the determination process

After operation of the pupal wings of Sy sy-animals, a considerably greater percentage of wings shows the higher degrees of reduction of the central field than after operation of wild type (sy sy) moths. This result throws some light on the action of the gene Sy. A certain stage of the spreading process will be more likely to be hit by the operation the longer it lasts. Therefore, the stages

determining a very small central field are retained a longer time in Sy sy-animals than in sy sy, or, in other words, the course of the determination stream is slowed down in Sy sy-animals. In what way this effect is accomplished, whether by an action on the impetus of the streaming process itself, or by an action on the substrate in which the process takes place can be answered by the following consideration. Certain phases of the spreading process seem always to be passed particularly slowly, and the corresponding situation of the bands is particularly often realized in the cauterization experiments. The same distance between the symmetrical bands which is normally found in Sy sy-animals, is relatively often induced in wild type animals after heat treatment in the sensitive period, or after cauterization. Several other places on the wing are also very likely to be occupied by the bands in these experimental animals. Therefore, the course of the determination current does not seem to be uniform, but retarded at certain regions of the wing. Those results suggest that the substrate of the current is not homogeneous, but at certain regions there seem to be thresholds whose transgression requires a certain time. Evidence for the occurrence of inequalities in the structure of the pupal wing is furnished by the observation of Koehler (1932) that already in the prepupa, long before the determination stream takes place, folds in the wing epithelium appear exactly in the regions where subsequently the symmetrical bands will be developed.

In the operations on Sy sy wings, certain phases of the beginning of the determination stream are very often encountered. It seems, therefore, that the gene Sy causes a retardation of the determination current by some action on the inequalities of the substrate.

Whether the gene *Syb* acts on the impetus of the current or on the resistance of the substrate, is not yet known. It is noteworthy, that the inheritance of the factor *Syb* forms an instance of the phenomenon of "maternal inheritance" (Kuehn and Henke, 1936). In reciprocal crosses between *Syb Syb* and *Syb syb* moths, the phenotype of the offspring is not entirely determined by their own genes, but a certain influence of the genotype of the mother has been observed: the offspring originating from a cross *Syb Syb* mother $\times$ *Syb syb* father has a broadened central field as compared with animals descended from a *Syb syb* mother. This fact tends to indicate that the manner of action of the gene *Syb* must be complicated. In some way it must influence the determination process causing the size of the central field. On the other hand, it may act at such an early stage as the unreduced egg cell. The gap between the two times of action which can be ascribed to this gene remains to be filled.

The results of the cauterizing experiments, combined with the observations in genetical and temperature treatment experiments, give a physiological meaning to several of the conceptions derived by morphological analysis. The conception of a field bordered by bands has been established to be due, in the case of the symmetrical system, to a determination stream spreading over the wing surface. The region where the current stops is marked in the developed wing by the white zone of the symmetrical bands. The innermost dark line is a differentiation of the central field; the outermost dark zone, of the outer field. The area, over which the determination stream has passed becomes distinguished from the outside areas, as shown in many instances (e.g., in *P. cynthia*) by a difference of

coloration. But even in cases where this difference between central field and outer-field is not developed normally (e.g., *Ephestia*), it can be shown to exist under experimental conditions. Two genes are known in *Ephestia* (Whiting, 1919; Kuehn, 1937, 1939b) which darken the central field only, without affecting the outer-fields. Another gene described by Whiting (1919) makes the outer-fields (external and internal field) sooty, giving to the central field, however, a lighter coloration than usual. Strohl and Koehler (1934) obtained white scales inside the central field, but not in the outer fields, by treatment of early *Ephestia* pupae with CO_2 .

The fact that the determination stream reaches the upper side of the wing from the fore and from the hind edge suggests a center for the spreading process on the under side of the wing—a fact confirming the developmental unity of the symmetrical systems on upper and under side of the wing.

The heterogeneities found in the substrate of the spreading process may perhaps be regarded as a physiological equivalent for the areas of the wing where pattern elements are particularly likely to be found, the pattern loci.

The determination of pattern elements in P. cynthia

Comparable conditions have been found by Henke (1933a) for the symmetrical system of *P. cynthia* by means of operations on the imaginal wing buds of late caterpillars. If a cut is made in the wing imaginal bud, the pattern of the adult wing corresponds, to a certain degree, to the results obtained after cauterization of *Ephestia* wings at the first day of the pupal stage. The size of the central field becomes diminished, and the operation scar is always situated outside the

central field, the symmetrical bands forming a sharp boundary of the central system against the operated area as well as against the outer-field. This behavior leads in the hind-wing to a withdrawal of the symmetrical system towards the hind margin of the wing. The connection between the central fields of upper and under side remains always uninterrupted. In the fore-wing, the central field may become divided at its narrowest place, giving rise to two symmetrical systems at the hind and fore edge of the wing. The pictures obtained in those experiments resemble closely those found in *Ephesia* after cauterization in the region of the anal vein, so that the same explanation of a determination stream originating at the under side of the wing and passing to the upper side around the fore and hind edge can be applied. At the under side of the fore-wing a proximal symmetrical band may appear after operation, which is not developed under normal conditions, the central field reaching the base of the wing in unoperated specimens.

If a part of the symmetrical system is strongly reduced, but not yet completely eliminated, the "pauperization," already mentioned in *Ephesia*, is observed, meaning that the innermost zones of the system disappear first and the outermost white line last in the course of progressive reduction. The outermost pink stripe, which may or may not be lacking independently of the other elements, forms occasionally an exception, indicating its developmental independence from the symmetrical system, like the corresponding outermost dark stripe of the bands of *Ephesia*. The symmetrical bands of *P. cynthia* as well as of *Ephesia* are shown in this way to be combined elements, the outermost zone being a differentiation of the outer-field. The border of the sym-

metrical system is in both cases constituted by the white line.

A similar analysis of the factors active in development has been undertaken for the discal ocellus of *P. cynthia* in the experiments of Henke. A certain area of epithelium which will afterwards form the ocellus is already determined in the late caterpillar, and after removal of this "anlage" no ocellus is formed. If, however, some of the ocellus-forming material is left, it regulates into an entire ocellus, indicating that its arrangement into different zones is not yet accomplished. This "anlage" recalls an harmonic equipotential system in so far as it is able to form two or even several complete ocelli after being cut into several parts by the operation. In reduced ocelli, the transparent center and the white zone may be lacking leaving only a yellow spot, conforming to the pauperization rule. The black line bordering only the foremost half of the ocellus, although belonging to the ocellus in its shape, resembles much more the black symmetrical band in its coloration behavior, as already mentioned above. The ocellus therefore can be regarded as another instance of a combined pattern element.

For the pattern elements apart from the central system a similar determination by a spreading process has been assumed, because of the morphological observation that all of them can be conceived as fields or as field border differentiations. No experimental evidence for this view is, however, available. For the ocellus, a similar kind of determination seems likely because of several similarities between ocellus and central system (e.g., concentric arrangement and "pauperization").

Other similarities suggesting also a similar origin have been observed in the behavior of the central shadow. The part of the central field distal to the central

shadow is sometimes distinguished in coloration from the proximal part, a case found in several Saturnid species and also in *Ephestia* under the influence of a gene *df* (Kuehn and Henke, 1935). Furthermore, in *Abraxas* the row of dark spots representing the central shadow changes its position in the central field after heat treatment at a certain sensitive period (Kuehn and von Engelhardt, 1936). Both observations support the view that the central shadow is a border differentiation between two differing fields, and the similarities of these facts to the well-known behavior of the symmetrical system makes a similar origin not unlikely.

Mitosis pattern

After the sensitive periods have passed, the determination of the wing pattern is completed. Subsequent treatment of the wing by operations, by temperature shocks, or by chemicals leads to abnormalities in scale structure and color production, but not to changes in the distribution of differently colored areas in the wing; that is in the general color pattern.

The first visible effect of the determination process is a peculiar distribution of cell divisions in the wing epithelium at a time immediately following the determination stream (Koehler, 1932; Braun, 1936). At this time, two waves of mitoses pass over the wing from the base towards the margin. In the histological description of the scale formation in *Ephestia* (Koehler, 1932; Stossberg, 1937), it has been shown that before the outgrowth of the scales, every scale-forming cell undergoes two differential mitoses. The same has been shown for *Rhopalocera* by Sueffert (1937). The first of the mitosis waves passing over the wing involves divisions of common hypodermis cells and the first differential divisions of the scale-forming cells. The second wave is constituted of second

differential divisions of scale-forming cells only (Braun, 1936). Koehler as well as Braun observed that those cell divisions are particularly frequent in the areas which later on will develop into dark pattern elements. The phenomenon has therefore been called "mitosis pattern." Both waves show maximal mitosis frequencies in the subsequently dark areas, resulting in a greater number of smaller cells per unit wing surface in the later dark areas and accordingly in a higher number of scales in the dark areas in the complete wing. That this mitosis pattern is a direct effect of the determination process has been proved by Braun (1936), who found the areas of maximal cell divisions shifted, according to the subsequently accomplished pattern, after heat treatment in the sensitive period and in presence of the gene *Sy*. Heat treatment in the sensitive period, besides shifting the mitosis pattern, arrests mitoses up to 24 hours, while cells already dividing finish their mitoses more slowly (Braun, 1939).

Histological differentiation of scales of different type

After this period of the cell divisions, the outgrowth of the scales begins, which has been described by Koehler (1932), Stossberg (1937), and Sueffert (1937). No differences in the behavior of the later differently colored and shaped scales could be found by histological methods (see also Koehler and Feldotto, 1937). However, Braun (1939) proved by the iodine-zinc chloride method of Schulze and by the difference in the time necessary for dissolving the scales by concentrated H_2SO_4 , that the parts of the wing which later are lighter in color, are at a certain period of differentiation already more chitinized than the subsequently dark areas. This fact accounts for the "relief stage," first detected and interpreted by Goldschmidt

(1920) in several species of butterflies and moths and lately found by Braun (1939) in *Ephestia*. If the still unpigmented pupal wing is removed from its sheath and dried, the subsequently dark scales, owing to their lesser chitinization, collapse, whereas the more chitinized later white scales remain inflated, showing a negative of the pattern in relief. Goldschmidt, interpreting this fact as due to different developmental velocities of the different kinds of scales, accounts for the different pigmentation by assuming that chromogens are present in the hemolymph at certain distinct times only, and that they can enter only the scales not yet entirely chitinized at this time. By showing that in the relief stage and even a considerable time before its appearance, only the less chitinized, i.e. the subsequent dark scales, give a pigmentation when treated with tyrosine, Braun (1939) gave strong support to this view. Goldschmidt (1938) tried also to connect the occurrence of the relief stage with the preceding mitosis pattern, in pointing out that the later dark areas undergo cell divisions at a time when the other wing cells have already undergone all their cell divisions, and that they can therefore be regarded as delayed in development.

The effect of the determination does not only consist in a different pigmentation, but also in a different shape of the scales in different areas. As Kuehn and Henke (1932) have shown, a certain pigmentation in the scales of *Ephestia* is always accompanied by a certain typical shape and structure, the dark scales being always higher and more slender than the white ones. If a change in the intensity or the size of a pattern element occurs under experimental conditions, the shape of the scales is changed according to their pigmentation. The determination, therefore, does not only account for differences

in pigmentation, but also in structure of the scales. The problem in this way becomes a morphogenetic one. This is particularly evident in the case of the blue iridescent scales often found in Lepidoptera. Their color, as Sueffert (1929) has shown, is an optical color, caused by the interference of light waves with especially arranged internal chitinous structures.

During the period of scale differentiation, changes in the structure of the scales are induced by heat treatment. At the beginning of this time, a sensitive period for loss of scales has been found by Feldotto (1933) in *Ephestia*, and by Koehler and Feldotto (1935, 1937) in *Vanessa urticae*. Later on, the latter authors found a sensitive period for a change in the shape and structure of the scales, without changes in their pigmentation. Shape and size of the scales may also be altered by starvation in the larval period (Koehler, 1940b).

Shortly before hatching, the pigmentation of the scales takes place. Different colors appear first at different times (Goldschmidt, 1923; Henke, 1933a). In the dark pattern elements of *Ephestia*, the pigmentation process appears to proceed from the base of the wing towards the distal edge (Koehler, 1932), like the mitosis pattern and the chitinization of the scales.

The different time of appearance of the different pigments leads to a peculiar behavior of the wing color of *P. cynthia* in the case of interference between different systems. In cases of reduction of the central field after operation, the ocellus often breaks partly through the symmetrical bands, so that certain areas of the wing are situated in the ocellus as well as in the band. The question is which kind of coloration shall prevail in those areas, the coloration belonging to the ocellus or to the band? Actually the

scales assume that one of the two possible colorations that is first formed in development, notwithstanding for which of the two systems it is characteristic (Henke, 1933a).

Inhibition of the development of determined pattern elements

Immediately before the pigment appears in the wing, a sensitive period for pigmentation occurs. By heat treatment during this sensitive period, only the pigment content of the scales is changed, without any corresponding change in the shape of the scales (Feldotto, 1933; Koehler and Feldotto, 1935). In the sensitive periods of Lepidoptera, therefore, three larger parts can be distinguished. After treatment in the first part of the pupal life, the determination of the pattern and the size of the systems constituting the pattern is changed. In the second part, the forming and the differentiation of the scales is influenced, while in the third part, only the pigmentation can be affected.

A certain number of genes have been described in *Ephestia* that influence the shape and size of the single scales (von Finck, 1938), the distribution of the pigments in the single scales (Kuehn and Henke, 1932), and the color of the scales (Kuehn and Henke, 1929). The mutation *b* (Whiting 1919; Kuehn and Henke, 1929) causes all light pattern scales which are relatively broad in shape to be replaced by the characteristic slender dark pigmented pattern scales, except for the white parts of the symmetrical bands and of the central spot. In *dz dz*-animals (Kuehn 1939b) a similar replacement of light pattern scales by dark pattern scales takes place, but in this case it is restricted to the central field. A mutation "*he*" causes in homozygous condition a weaker pigmentation in all scales of the wing.

In producing this effect, an alteration of the chitinization process may play a rôle (Kuehn, 1937, 1939a). The phenotypes caused by the genes *he* and *b* have been found to develop autonomously, if grafts of larval skin were transplanted into the fat body of wild type animals (Kuehn and Piepho, 1940). Genes influencing the pigmentation of the scales have also been found in numerous other species of Lepidoptera (see review by Ford, 1937).

A certain boundary is set to the effectiveness of the morphological pattern analysis by the fact that elements which are determined by or at least belong to the potentialities of a certain species, may not become actually developed. In this case experiment sometimes does show the existence of a normally lacking element. Several instances of this kind which seem to be caused by different mechanisms have been described.

No pattern is visible on the under side of the fore-wing of *Ephestia*. It seems, however, likely that it has been determined, as an origin of the determination stream at the under side of the wing is suggested by the direction of its flow, and as the mitosis pattern has been found on the under side of the wing by Koehler (1932). Close inspection reveals that the dark and white scales, which form the pattern elements, are not developed on the under side. It is covered with "ground scales" only, a type of scale which is present on the upper side also, forming the underground and not reaching the surface, so that they do not contribute to the pattern (Kuehn and Henke, 1932). A few pattern scales are, however, present at the tip of the under side and here they actually are arranged so as to form the beginning of the distal symmetrical band.

Another instance of an apparent absence of determined pattern elements is found in the mutation *b* (black, Whiting, 1919;

Kuehn and Henke, 1929) in *Ephestia*. In homozygous *bb* animals, all scales, except the white ones belonging to the symmetrical bands and to the central spots, are replaced by black pattern scales, so that the dark pattern elements cannot be distinguished. However, the presence of the dark central spots can be shown by the interaction of the gene *s* (Whiting, 1919) which lightens the central field, showing clearly the central spots, or by treatment of *bb* wings with ultraviolet light at a certain period (Strohl and Koehler). Under the latter influence, light scales are developed in the irradiated area, and the dark central spots appear clearly in the lighter surroundings. The fact that in *bb* animals the dark pattern elements are present and only covered by the general black pigmentation, has already been seen by Koehler (1932) in observing the course of pigmentation in black animals. In the pupal wing, the pigmentation begins at the normal time in the normal manner, the dark pattern elements becoming colored against a lighter background. Afterwards a stream of black pigment spreads from the base of the wing to the edge, coloring the background dark, so that the pattern elements cannot be distinguished. It is noteworthy that, in this case, the dark scales of the background show the same morphological type as the dark scales in the pattern elements, so that the same coloration is accompanied by the same structure of the scales, but not by the same time of pigmentation.

On the other side, a pattern element may not be visible because it is covered by another one. This case seems to be present relatively often, due to the occurrence of identical pattern loci for different elements. This possibility has already been described for the internal shadow of *P. cynthia*, which becomes visible when

the proximal symmetrical band is removed.

Another possibility has been described by Koehler and Feldotto in their modification experiments with *V. urticae* and *V. io* (1935). In these animals, certain elements may become so reduced after heat treatment at a certain time of their sensitive period that they are entirely lacking. The opposite has also been observed—the appearance *de novo* of pattern elements after treatment at the time in which a heat shock has the maximum effect on this pattern system. The central field of *V. urticae* is represented by two large black spots at the fore and hind parts of the wing. After heat treatment at the maximum of their sensitive period, the two spots can become united by a line of black scales, the central field forming in this way a dark band across the whole wing. In the closely related species *V. io* the corresponding system consists of one dark spot at the fore part of the wing only. After a heat shock applied to animals of this species at the time of maximum effect of the sensitive period for the central field, a dark spot in the hind part of the wing appears, corresponding to the hind spot normally present in *V. urticae*. Its behavior resembles that of the foremost part of the central field so much that no doubt exists as to its belonging to the same system.

All these facts show clearly that the developmental possibilities of a certain species of Lepidoptera may be much larger than the pattern ultimately developed, and that different factors during development may be able to abolish their expression. The last case is very interesting in so far as here the suppression of a pattern element seems to be due to the nature of the determination process under natural conditions. The potential pattern element can appear only if the deter-

mination process is raised to a higher level by external influences.

Rhythmical patterns

Hitherto, only pattern elements have been dealt with that can be regarded as field structures or field border differentiations. Actually systems of this kind represent the majority of the elements forming the Lepidopteran wing pattern, but they are not the only kind. Sueffert (1927, 1929) has described a certain kind of rhythmically repeated elements (small lines or dots) under the name "purling patterns." Henke (1936) distinguished two kinds of rhythmical patterns: spreading rhythms, characterized by an obvious arrangement around a virtual center, and simultaneous rhythms. Henke is inclined to regard the first kind as caused by a chemical arrangement process like the *Liesegang* phenomenon, the concentric arrangement of precipitates in a colloidal medium, if one reagent diffuses through it from a center, the other one being dissolved in the colloid. The simultaneous rhythms may perhaps be regarded as caused by growth rhythms.

No experimental material is thus far available to confirm these views. Koehler and Feldotto (1935) found a distinct heat sensitive period for the rhythmical elements on the under side of the wing of *V. urticae*. Even on the upper side, where no rhythmical pattern is developed normally, rhythmical elements may appear after heat treatment at the time of maximum effect of their sensitive period. The occurrence of a sensitive period suggests perhaps an origin not too different from the origin of the field patterns.

Dependent patterns

Finally, Sueffert described a type of "dependent elements," i.e. elements which show a clear morphological dependence

upon the structure of the wing, the veins, and the margin. The most conspicuous instance of this kind of pattern is colorations of the veins. However, most of the other elements show a certain dependence upon the wing structure too, as, e.g., the discal elements, dependent in situation upon the transverse discal vein; the marginal spots in *Ephestia*, situated always at the margin between the veins; and the symmetrical bands of *Ephestia*, which are broader on the veins than between them, assuming an arrow-like shape on every vein.

An experimental analysis of a dependent behavior has been possible for the pseudo-marginal spots on the hind-wing of *P. cynthia* (Henke, 1933a). They represent a row of spots running parallel to the edge of the wing, situated in a proximal direction from the border line, always between the veins (cf. Fig. 1). This relation remains true even under experimental conditions. If a vein is shortened after an operation at the wing imaginal bud, the corresponding spots unite to form a single spot. If new veins are formed the spot crossed by it divides into two. These observations would fit the conception of a direct dependence of the marginal spots upon the veins. If, however, a vein does not reach the margin of the wing entirely, but ends near it, the nearest marginal spot extends in the direction towards the vein (Fig. 9), occasionally even so far that the vein may enter the spot without dividing it. Close inspection of the surrounding area solves this apparent contradiction. The pseudo-marginal spots are situated in a light colored area, the border-field, which is sharply distinguished in coloration from the external field and by a line from the marginal field. The boundary between border-field and external outer-field in normal individuals is slightly bent on the veins in the direction towards the

wing margin. If, however, the vein is shortened under experimental conditions, this boundary follows the vein, forming evaginations in its direction. The marginal spots always maintain a constant distance from this boundary, whether it is bent in a proximal or in a distal direction. This behavior explains the evaginations of the spots under experimental conditions, but not their division by the veins in normal cases. They could be bent in a distal direction like the field boundary and maintain their connection. Therefore, a second factor, the maintenance of a constant distance from the borderline or from the margin is to be assumed. In this

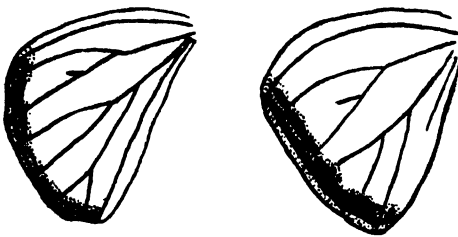


FIG. 9. ALTERATIONS OF THE VEINS AND OF THE SUB-MARGINAL PATTERN ELEMENTS AFTER OPERATION OF THE IMAGINAL BUD OF THE HIND WING OF *PHILOMIA CYNTHIA*

After Henke 1933a.

way, the pseudosubmarginal spots appear as differentiations of the border-field, which tend to maintain a constant distance from the proximal and distal boundary of this field. The division of the marginal spots is not due to a direct influence of the veins on the spots, but an indirect one, primarily acting on the shape of the field producing the spots.

Koehler (1940b) described the occurrence of supernumerary cubitus veins in *Ephestia*. If such a supernumerary vein reaches the margin of the wing, two marginal spots are formed instead of one as in normal animals. If, however, the supernumerary branch unites with its neighbor before reaching the margin,

only the normal marginal spot is present. Koehler suggests that the position of the marginal spots may be determined by the situation of the underlying blood lacunae, which determine on the other hand also the course of the outgrowing tracheae.

CONCLUSIONS

The analysis of the development of the wing pattern of *Lepidoptera* is far from being completed. We know about the determination of at least one pattern system, the central symmetrical system, by a spreading process in the wing epithelium. But how this process causes its first morphological effect, the arrangement of mitotic figures according to the later developed pattern, is still unknown. Also the gap between this mitosis pattern and the formation of the final pattern consisting of differently shaped and colored scales remains to be filled. In a general way it can, however, be claimed that some of the chief principles of pattern determination have been established. The investigation started with a morphological analysis of the pattern variability in different groups and succeeded in describing and connecting them with the aid of relatively few conceptions, among which the conception of pattern systems and pattern loci are outstanding. Experimental analysis has given evidence for the physiological processes underlying these conceptions. The systems consist of different pattern elements which are caused by the same developmental process and, therefore, react in the same way to external (temperature) and internal (genes) influences. In the best analyzed case, this developmental process is a determination stream spreading over the wing surface. Also in most of the other cases it is best regarded as the formation of fields and field border differentiations. The conception of pattern loci may find its

developmental equivalent in the observed heterogeneities in the wing epithelium which form areas of higher and lower resistance for the flow of the determination current. With the aid of these experimental facts, the morphological analysis is able to give evidence for the developmental processes in wings of species which have not been analyzed experimentally.

On the other hand, the analysis has furnished major contributions to fundamental problems of general biology, mainly the question of gene action. A great number of genes influencing different aspects of pattern formation have been studied and light has been thrown on

their influence on the developmental processes, the steps where they exert their action and their interaction with external influences, chiefly temperature alterations. Besides this, a suitable material has been found for the study of several developmental phenomena, as, e.g., the collaboration of parts of different origin in the formation of a single morphological trait.

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LIST OF LITERATURE

- BEHREND, J. 1935. Ueber die Entwicklung des Lakunen- Ader- und Tracheensystems waehrend der Puppenruhe im Fluegel der Mehlmotte *Ephestia kuehniella* Zeller. *Ztschr. Morph. Oekol. Tiere*, 30: 573-596.
- BRAUN, W. 1936. Ueber das Zellteilungsmuster im Puppenfluegelepipithel der Mehlmotte *Ephestia kuehniella* Z. in seiner Beziehung zur Ausbildung des Zeichnungsmusters. *Arch. f. Entwmech.*, 135: 494-520.
- . 1939. Contributions to the study of development of the wing-pattern in Lepidoptera. *Biol. Bull.*, 76: 226-240.
- . 1939a. Disturbances in the process of cell-division in the pupal wing of the flour-moth *Ephestia kuehniella* as result of heat-treatment. *Cytologia*, 10: 40-43.
- CLAUBEN, K. H. 1937. Kreuzungsanalyse des Zeichnungsmusters zweier Staemme von *Ephestia kuehniella* Z. ("Siebenbuergen" und "Goettingen N VI"). *Ztschr. f. ind. Abst. u. Vererbgs.*, 72: 488-500.
- FELDOTTO, W. 1933. Sensible Perioden des Fluegel-musters bei *Ephestia kuehniella* Zeller. *Arch. f. Entwmech.*, 128: 299-341.
- VON FINCK, E. 1938. Genetische Untersuchungen ueber die Schuppengroesse und Schuppenform bei der Mehlmotte *Ephestia kuehniella* Z. *Ztschr. f. ind. Abst. u. Vererbgs.*, 74: 161-201.
- FORD, E. B. 1937. Problems of heredity in the Lepidoptera. *Biol. Rev. Cambridge Philosoph. Soc.*, 12: 461-503.
- GEISEL, H. 1936. Entwicklungsdauer, Fluegel-laenge und Vitalitaet ingezuehteter Mehlmottenstaemme und ihrer Kreuzungen. *Ztschr. f. ind. Abst. u. Vererbgs.*, 71: 382-416.
- GEROULD, J. H. 1927. Studies in the general physiology and genetics of butterflies. *QUART. REV. BIOL.*, 2: 58-78.
- GOLDSCHMIDT, R. 1920. Untersuchungen zur Entwicklungsphysiologie des Fluegelmusters der Schmetterlinge. *Arch. f. Entwmech.*, 47: 1-24.
- . 1923. Einige Materialien zur Theorie der abgestimmten Reaktionsgeschwindigkeiten. *Arch. mikr. Anat.*, 98: 292-313.
- . 1927. Physiologische Theorie der Vererbung. *Berlin*.
- . 1938. *Physiological Genetics*. McGraw-Hill Book Co.
- HENKE, K. 1928. Ueber die Variabilitaet des Fluegel-musters bei *Larentia sordidata* F. und einigen anderen Schmetterlingen. *Ztschr. Morph. Oekol. Tiere*, 12: 240-282.
- . 1933a. Untersuchungen an *Philosamia cyathia* Drury zur Entwicklungsphysiologie des Zeichnungsmusters auf dem Schmetterlingsfluegel. *Arch. f. Entwmech.*, 128: 15-107.
- . 1933b. Zur vergleichenden Morphologie des zentralen Symmetriesystems auf dem Schmetterlingsfluegel. *Biol. Zentralbl.*, 53: 165-199.
- . 1933c. Zur Morphologie und Entwicklungsphysiologie der Tierzeichnungen. *Naturwiss.*, 21: 633-690.

- HEINKE, K. 1935. Entwicklung und Bau tierischer Zeichnungsmuster. *Verhandl. Deutsch. Zool. Ges.*, 1935: 176-244.
- . 1936. Versuch einer vergleichenden Morphologie des Fluegelmusters der Saturniden auf entwicklungsphysiologischer Grundlage. *Nova Acta Leopoldina*, 4, Nr. 18, Halle a. S.: 1-137.
- . 1937. Untersuchungen zur Entwicklungsphysiologie und Genetik der Fluegelform bei der Mehlmotte. *Biol. Zentralbl.*, 57: 449-507.
- HUGOEL, E. 1933. Ueber das genetische Verhalten der weissen Distalbinde und ihre genetischen Korrelationen zu anderen Merkmalen auf dem Vorderfluegel der Mehlmotte *Ephestia kuebniella* Zeller. *Arch. f. Entwmech.*, 130: 202-242.
- KOEHLE, W. 1932. Die Entwicklung der Fluegel bei der Mehlmotte *Ephestia kuebniella* Zeller mit besonderer Beruecksichtigung des Zeichnungsmusters. *Ztschr. Morph. Osk. Tiere*, 24: 582-681.
- . 1940a. Der Einfluss verschiedenen Ernahrungsgrades auf aeuessere Koerpermerkmale, auf die Entwicklungsgeschwindigkeit, Lebensdauer und Fortpflanzungsfachigkeit von *Ephestia kuebniella* Z. *Biol. Zentralbl.* 60: 34-69.
- . 1940b. Erbliche Ausfallserscheinungen und Regulationen am pupalen Fluegeltracheensystem von *Ephestia kuebniella* Z. *Biol. Zentralbl.* 60: 348-367.
- , and W. FELDOTTO. 1936. Experimentelle Untersuchungen ueber die Modifikabilitaet der Fluegelzeichnung, ihrer Systeme und Elemente in den sensiblen Perioden von *Vanessa urticae* L., nebst einigen Beobachtungen an *Vanessa io* L. *Arch. Julius Klaus Strifg.*, 10: 313-453.
- , and —. 1937. Morphologische und experimentelle Untersuchungen ueber Farbe, Form und Struktur der Schuppen von *Vanessa urticae* und ihre gegenseitigen Beziehungen. *Arch. f. Entwmech.*, 136: 313-399.
- KUEHN, A. 1926. Ueber die Aenderung des Zeichnungsmusters von Schmetterlingen durch Temperaturreize und das Grundschema der Nymphalidenzeichnung. *Nachr. Ges. Wiss. Goettingen, Math.-Phys. Kl.*, 120-141.
- . 1932a. Zur Genetik und Entwicklungsphysiologie des Zeichnungsmusters der Schmetterlinge. *Nachr. Ges. Wiss. Goettingen, Math.-Phys. Kl.*, 312-335.
- . 1932b. Entwicklungsphysiologische Wirkungen einiger Gene von *Ephestia kuebniella*. *Naturwiss.*, 20: 974-977.
- . 1934. Genetische und entwicklungsphysiologische Untersuchungen an *Ephestia kuebniella* Z. *Ztschr. f. ind. Abst. u. Vererbgs.*, 67: 197-200.
- . 1936a. Versuche ueber die Wirkungsweise von Erbanlagen. *Naturwiss.*, 24: 1-10.
- KUEHN, A. 1936b. Ueber die Wirkungsweise von Erbanlagen, insbesondere ueber Phaenokopien und hormonale Genwirkungen. *Comptes Rendus XII^e Congres Internat. Zool., Liebronne*: 5-18.
- . 1937. Entwicklungsphysiologisch-genetische Ergebnisse an *Ephestia kuebniella* Z. *Ztschr. f. ind. Abst. u. Vererbgs.*, 73: 419-455.
- . 1939a. Ueber die Mutation hc(gehemmte Ausaeerbung) bei der Mehlmotte *Ephestia kuebniella* Z. *Ztschr. f. ind. Abst. u. Vererbgs.*, 77.
- . 1939b. Ueber eine geschlechtsgekoppelte Mutation des Zeichnungsmusters(dz) bei *Ephestia kuebniella* Z. *Biol. Zentralbl.*, 59: 347-357.
- , and M. VON ENGELHARDT. 1933. Ueber die Determination des Symmetriesystems auf dem Vorderfluegel von *Ephestia kuebniella* Z. *Arch. f. Entwmech.*, 130: 660-703.
- , and —. 1936. Ueber die Determination des Fluegelmusters bei *Abraxas grossulariata* L. *Nachr. Ges. Wiss. Goettingen, Math.-Phys. Kl.*, *Nachr. a. d. Biol.* 2: 171-199.
- , and —. 1937. Ueber eine melanistische Mutation von *Prychopoda seriata* Schrk. (at → At) und die Abhaengigkeit der at und At zugeordneten Merkmale von Aussenbedingungen. *Biol. Zentralbl.* 57: 329-347.
- , and —. 1940. Ein das Fluegelmuster beeinflussender Letalfaktor bei *Prychopoda seriata*. *Biol. Zentralbl.*, 60: 561.
- , and K. HEINKE. 1929-1936. Genetische und entwicklungsphysiologische Untersuchungen an der Mehlmotte *Ephestia kuebniella* Zeller. *Abhandl. Ges. Wiss. Goettingen Math.-Phys. Kl.*, vol. 15: Nr. 1, 1929 (I-VII); Nr. 2, 1932 (VIII-XII); Nr. 3, 1936 (XIII and XIV): 1-272.
- , and —. 1935. Ueber einen Fall von geschlechtsgekoppelter Vererbung mit wechselnder Merkmalsauspraegung bei der Mehlmotte *Ephestia kuebniella* Zeller. *Nachr. Ges. Wiss. Goettingen, Math.-Phys. Kl., Fachgr. Biol.*, Neue Folge 1: 247-259.
- , and H. PIEPHO. 1940. Ueber die Ausbildung der Schuppen in Hauttransplantaten von Schmetterlingen. *Biol. Zentralbl.*, 60: 1-22.
- KUNTZE, H. 1935. Die Fluegelentwicklung bei *Philosamia cynthia* Drury, mit besonderer Beruecksichtigung des Gaeaders, der Lakunen und der Tracheensysteme. *Ztschr. Morph. Oskol. Tiere*, 30: 544-572.
- MAGNUSSEN, K. 1933. Untersuchungen zur Entwicklungsphysiologie des Schmetterlingsfluegels. *Arch. f. Entwmech.*, 128: 447-479.
- SCHWANWITZ, B. N. 1924. On the ground-plan of wing-pattern in Nymphalids and certain other families of the Rhopaloceros Lepidoptera. *Proc. Zool. Soc., London*.

- SCHWANWITZ, B. N. 1925. On a remarkable dislocation on the components of the wing-pattern in the Satyrid genus *Pierella*. *Entomologist*, 58.
- . 1928. Pierellisation of stripes in the wing-pattern of the genus *Rhaphicera*. *Zschr. Morph. Oekol. Tiere*, 11: 1-12.
- . 1929a. Evolution of the wing-pattern in palaearctic Satyridae. I. Genera *Satyrus* and *Oeneis*. *Zschr. Morph. Oekol. Tiere*, 13: 559-654.
- . 1929b. Two schemes of the wing-pattern of butterflies. *Zschr. Morph. Oekol. Tiere*, 14: 36-58.
- . 1931. Evolution of the wing-pattern in palaearctic Satyridae. II. Genus *Melanargia*. *Zschr. Morph. Oekol. Tiere*, 21: 316-408.
- , and G. N. SOKOLOV. 1934. On the wing-pattern of the genus *Lasbe* (Lepidoptera, Satyridae). *Acta Zool.*, 15: 153-181.
- SCHWARTZ, V. 1937. Ueber einen geschlechtsgebundenen Letalfaktor bei *Ephestia kuebniella* Z. *Biol. Zentralbl.*, 57: 347-354.
- . 1938. Ueber die Vererbung des Ausprägungsgrades der schwarzen Querbindenzeichnung auf dem Vorderflügel von *Ephestia kuebniella* Z. *Zschr. f. ind. Abst. u. Vererbgs.*, 74: 409-419.
- STOMBERG, M. 1937. Ueber die Entwicklung der Schmetterlingschuppen. *Biol. Zentralbl.*, 57: 393-402.
- STROHL, J., and W. KOEHLER. 1934. Experimentelle Untersuchungen ueber die Entwicklungsphysiologie der Flügelzeichnung bei der Mehlmotte. *Verhandl. Schweizer. Naturforsch. Ges. Zurich*, 1934: 367-370.
- , and —. 1935. Die Wirkung eines pleiotropen Gens auf Färbung, Lebensdauer und Fortpflanzungsfähigkeit bei der Mehlmotte *Ephestia kuebniella* Z. *Nachr. Ges. Wiss. Göttingen, Math.-Phys. Kl., Nachr. a. d. Biol.*, 2: 31-55.
- STUBBS, A. E. 1938. Die Wirkungen verschiedener Reizung mit erhöhter Temperatur auf das Zeichnungsmuster zweier Stämme der Mehlmotte *Ephestia kuebniella* Zeller. *Zschr. f. ind. Abst. u. Vererbgs.*, 75: 233-255.
- SUEFFERT, F. 1925. Geheime Gesetzmässigkeiten in der Zeichnung der Schmetterlinge. *Rev. Suisse Zool.*, 32.
- . 1927. Zur vergleichenden Analyse der Schmetterlingszeichnung. Vorläufige Mitteilung. *Biol. Zentralbl.*, 47: 385-413.
- . 1929. Morphologische Erscheinungsgruppen in der Flügelzeichnung der Schmetterlinge, insbesondere die Querbindenzeichnung. *Arch. f. Entw. u. Vererbgs.*, 120: 299-383.
- . 1937. Die Geschichte der Bildungszellen im Puppenflügelepitheel bei einem Tagsschmetterling. *Biol. Zentralbl.*, 57: 615-628.
- WHITING, P. W. 1919. Genetic studies on the Mediterranean flour-moth *Ephestia kuebniella* Zeller. *J. exper. Zool.*, 28: 413-441.
- . 1927. Reversal of dominance and production of a secondary sexual character in the Mediterranean flour-moth. *Amer. Naturalist*, 61: 450-456.
- WULKOPF, H. 1936. Hitze- und Frostreize in ihrer Wirkung auf das Flügelmuster der Mehlmotte *Ephestia kuebniella* Zeller. *Arch. f. Entw. u. Vererbgs.*, 134: 209-223.





THE LABORATORY POPULATION AS A TEST OF A COMPREHENSIVE ECOLOGICAL SYSTEM

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INTRODUCTION

THE time is ripe for a careful and critical scrutiny of certain aspects of the terminology issue in ecology. If judiciously done such scrutiny should furnish an over-view of basic ecological concepts and principles. However, this is not a simple task. It would be easy to hold that all ecological terminology is bad; that the field is not yet ready for a nomenclature of its own; that such a nomenclature can never be of value. It would be equally easy to hold that the ecologists have been unusually perspicacious in matters of terminology and that ecologic terms are both meaningful and empirical. Unfortunately, neither position appears to be sound. It must be granted immediately that any system of ecological terminology that is brief, skeletal yet general is much to be desired. It is apparent that, even if capable of development, such a system is yet to be discovered. There are good reasons for this. The primary ones seem to be (a) that the environmental relationships of organisms in nature are innately complex, and (b) that the evidence necessary to delineate these relationships is sadly lacking.

The present treatment is in no sense a discourse on esoteric terminology. In fact that is a subject about which the author is both skeptical and critical (Park, 1939a). However, I have been interested for over

a decade in problems concerned with the experimental and statistical biology of populations and have seen the growth of a good deal of respectable information collected primarily by using insects and microörganisms as experimental material. (For key references see Allee, 1931; Bodenheimer, 1938; Gause, 1934; Park, 1939; Pearl, 1925; Thompson, 1939; and Wright, 1931.) It seems to me that much of this subject matter is ecological in character. This lends impetus to the present paper in which an attempt will be made to apply certain facts and concepts gleaned from population research to a general ecologic system intended to fit a diverse series of natural field communities.

Although the laboratory population studies have been approached from several points of view they share, in the main, certain common properties. Some of these properties may be listed as follows:

(1) There is an attempt in all these studies to express the results in *quantitative* terms. This is a desirable, though not always possible, end-product in any ecological venture.

(2) There is essentially a complete absence of terminology in the studies. This may mean that the results are not too well integrated. It may also mean that this phase of ecology is free from the bias of prematurely coined terms and, by that token, poorly crystallized concepts.

(3) Most of the studies are concerned with important biological variables. Particularly well studied are (a) the factors contributing to population growth—fecundity, fertility, fission rate, success and rate of development; (b) the factors contributing to population decline—differential morbidity and mortality; and (c) the factors concerned with selection pressure. All these factors usually have been analyzed in the presence of differential population densities.

(4) There are certain theoretical generalizations that have grown out of, or along with, these studies. Some of these are far from polished; others are quite well established. For example, Pearl and Reed (1920) have shown that most populations follow a sigmoid curve of growth that they designate "logistic." A criticism of their ideas appears in a paper by Wilson and Puffer (1933). Volterra (1926), Lotka (1934), Nicholson (1933), Nicholson and Bailey (1935), Stanley (1932, 1932a), Thompson (1939), and others have emphasized the mathematics of competition and biotic interactions. Wright (1931), Haldane (1932), and Fisher (1930) have shown in statistical terms the necessity of treating problems of evolution as a phase of the biology of populations and thus have played the important rôle of merging certain aspects of genetics and ecology under a common biological denominator. Dobzhansky (1937) has applied some of these findings to field populations of *Drosophila pseudoobscura*. Allee (1931, 1940) has delineated the principle of aconscious cooperation to be discussed later and Emerson (1939) and Gerard (1940) have examined once more the population as a supra-organism. Bodenheimer (1938) and Gause (1934) have applied certain theoretical concepts to laboratory data. Hjort (1938) has viewed the population problem in terms of human values.

There appeared recently (1939) a book by Clements and Shelford entitled *Bio-Ecology*. This book has been the subject of much controversy among biologists. One finds among its reviewers (for examples, see Elton, 1940; Hutchinson, 1940) various opinions of its worth ranging from outspoken criticism to moderated praise. The criticisms take the form that the book is unscientific, lacks evidence to back up its concepts, is neither closely written nor well thought out, and is replete with meaningless terms. The praise takes the form that the book has important basic ideas, that it has been written by investigators familiar with a wealth of field material and that it represents a type of synthesis towards which ecology can move with profit.

It is my feeling that it will prove stimulating to select carefully certain of the basic concepts described in the Clements-Shelford book, discuss these concepts in abstract terms and then try to fit them with some of the data that have emerged from laboratory population studies. I think this will be instructive in several ways. First, it will provide a test for seeing if there are close parallels between a natural and an experimental population. Second, it may illuminate the workings of a complex field community since the laboratory populations provide a highly simplified yet complete biological system. Third, such an application will tend towards quantification of ecological phenomena since, in their final form, the laboratory studies are usually expressed in numerical terms. Fourth, there may be an opportunity to examine critically and realistically the meaning, or lack of meaning, of an ecological term when applied to a specific and fairly well analyzed example. It must be emphasized at once that the present article is not intended to pass judgment one way or another on the general

worth of the Clements-Shelford book. That would be presumptuous; in fact, there are many aspects of the book I shall not touch on. It is the hope that this paper will test some of the issues raised above and aid in clarifying the *modus operandi* of two types of biological associations—the natural community and the laboratory population. This paper will develop as follows: (1) a selection and definition of the important integrative concepts proposed by Clements and Shelford; (2) illustration of these concepts wherever possible using examples taken from the experimental population literature; and (3) a synthesis and discussion of the results. There will be no new terms introduced. From a certain point of view this may be considered a weakness in the paper. The reader may feel with justification that, after spending so much time on the Clements-Shelford system and critically evaluating it, the author should propose and develop a modification that he considers better. I agree heartily that that should be done but personally prefer to wait until ecologists have thought longer and more soundly about the matter. Undoubtedly, at a somewhat later date, someone will prepare such a synthesis. The experimental examples used in this paper will draw on work carried out primarily with the flour beetle, *Tribolium confusum*, and the fruit fly, *Drosophila melanogaster*. Other insect studies will be mentioned briefly where pertinent. The emphasis is placed on *Tribolium* and *Drosophila* because these species have been used extensively in population research and because the author is most familiar with them.

THE GENERAL BACKGROUND

In their book, Clements and Shelford introduce the reader to a series of ideas and working concepts that are really categories into which, in their opinion, the opera-

tional activities of all communities fall. One says "all communities" advisedly for it is maintained by the authors that these activities are similar processes whether found at work in a grassland, a freshwater community, or a marine pelagic community. The processes may and do vary in expression and importance from area to area but, nevertheless, are identifiable and operative wherever a natural grouping of organisms occurs. Obviously then these are the factors we wish to examine in this paper. In the present section these factors will be formalized and illustrated briefly; in the next section they will be related to experimental population studies. At the moment we shall consider the following viewpoints or factors: (1) the philosophical basis; namely, a climax community is a complex social organism; (2) the meaning of habitat; (3) the operational factors, action and reaction; and (4) the significance of aggregation when broken down into its component coactions, co-operation, disoperation, and competition.

The community as a social organism

Clements and Shelford adopt the view throughout their book that plants and animals are associated in natural units over the earth and in the water. These units, designated "biomes," are definable geographically, morphologically (stressing the fact that both animals and plants are integral components), operationally, and developmentally. The existence of such units has led the authors, along with many others, to the conclusion that the community, "... is more than the sum of its parts, that it is indeed an organism of a new order. . . ." It is considered, "... to be a complex organism, bearing something of the same relation to the individual plant or animal that each of these does to the one-celled protophyte or protozoan." (P. 21.) In short, the authors feel that

the biome is so real a biological entity that there has been established within it new levels of organization and integration that are lacking in the constituent parts. This idea need not be pursued now. We shall return to it later. Suffice it to say that the following positions among biologists seem to be recognizable at the moment: (a) that the concept is real and actually useful in the analysis of biological associations (Wheeler, 1913, 1923; Child, 1924; Emerson, 1939, 1939a; Gerard, 1940); (b) that the concept may be real but without pragmatic importance; and (c) that the concept is a product of loose-thinking and is genuinely misleading (Bodenheimer, 1938; Gleason, 1939). So far as I can determine, most of the human sociologists consider the idea to be archaic.

Habitat

The word "habitat" is used in a loose sense by most biologists and ecologists to mean simply the place or niche that an animal or plant occupies in nature. Thus the habitat of the wood-roach, *Parcoblatta*, is the forest floor and the under-bark of decaying logs; of the red-winged blackbird, a cattail marsh; and of a malarial parasite, the blood stream of a mammal and the gut and haemocoels of a mosquito. This is a helpful way to use habitat and the word will continue to be so applied. Clements and Shelford, however, restrict the word to include only the total physical and chemical environment of a population. They say,

"... habitat comprises all the physical and chemical factors that operate upon the community. Of these, water, temperature, light and oxygen are of vast importance to both plants and animals, and carbon dioxide to all holophytes and a few chlorophyll-bearing animals. The raw materials for food making by the plants are obviously habitat factors, but food itself is not. . . . As to the solutes themselves, some can be used by the animal directly, while others are available only, or usually, in combination. Sub-

stratum and bottom are of much significance for great numbers of aquatic animals, and soil is indispensable to most plants and of no little importance to many land animals." (P. 26-27.)

In this paper then we will view the habitat as a physical-chemical frame-work that supports, either directly or indirectly, the complete biota of its respective community. A single example will make the point. Near the end of the last century Möbias (1877) in a significant paper pointed out certain facts about the distribution and structure of an oyster community (biocoenose) in nature. Under the Clements-Shelford system the habitat of an oyster population would include such factors as the substratum; sea-water, both as a physical medium and a chemical solution, and pressure, light, temperature, salinity, hydrogen ion factors and so on. The habitat would not refer to a particular niche occupied by a single oyster nor would it imply anything about the biotic interactions within the oyster population. In the present paper we shall use habitat in the sense of Clements and Shelford. An interesting philosophical discussion of habitat has been published recently by Haskell (1940).

The cycle of action and reaction

It is apparent on purely logical grounds that if organisms live in a physical habitat such as has just been described there must be certain basic operations continually occurring between these two elements of the environment. Clements and Shelford regard these operations as the *primary* cycle of cause and effect within the community and designate those forces operating as action and reaction. By action is meant the influence impinged on the community or population by the habitat. By reaction is meant the influence impinged on the habitat by the community. Thus if community is represented by "C" and habitat

by "H" the definition can be symbolized as follows:

$$\begin{aligned}\text{Action} &= H \rightarrow C \\ \text{Reaction} &= H \leftarrow C \\ \text{The cycle} &= H \rightleftharpoons C\end{aligned}$$

A brief quotation will help:

"In the plant matrix of the land biotic community, the causal sequence is a fairly simple cycle. The action of the habitat as expressed in stimuli gives rise to responses on the part of the plant or community. These in turn operate on the habitat, producing reactions that modify it, and then again in turn its action on plant life follows" (*Bio-Ecology*, p. 30).

There are some inappropriate implications, however, in using the term "primary" in connection with this cycle. We know that there must be an original relationship between habitat and organism that, in truth, is a primary or *first* action-reaction cycle. But this is not to admit for a moment that later cycles are also primary. In reality they are secondary, tertiary, or higher in character and depend on the development and maturation of earlier action-reactions and coactions that have emerged in the population life-history during the interim. In my opinion, the system of Clements and Shelford does not differentiate too adequately these temporal and structural gradations in the action-reaction cycle. We shall return to the point when discussing the conditioning of flour by *Tribolium* populations.

Action and reaction are so obvious that numerous illustrations will immediately suggest themselves to the reader. The importance of the concept seems to lie in just this comprehensive fact: namely, that these ecological forces are operating irrespective of the type of community under consideration and thus are integrating phenomena common to all biological associations. Organisms in a community must adjust to actions of the habitat. Changes in climate, or substratum, or day to night,

or, in a littoral marine community, tide level are all habitat changes that may act on the population and induce an adjustment. We shall examine laboratory illustrations of these actions later. Likewise, reactions are easily noted. An excellent case is the influence of plants and animals on soils. Here, the community reacts on the habitat in one of three general ways: (a) reactions may give rise to new soils or contribute materials that eventually form soil; (b) reactions may protect the soil against, say, erosion, or trampling, or burrowing; and (c) reactions may change the texture, structure, or general character of soil to a noticeable extent (*Bio-Ecology*, p. 72). The importance of such processes need not be pursued.

Aggregation and its end effects

In any biological association there must be more than the primary cycle of action and reaction. Another cycle becomes established that has as its basis the aggregation or grouping of the plants and animals within a particular habitat. This is another way of saying that in a population the inter-individual responses between the members of that population are of great importance. These responses are designated by Clements and Shelford as "coactions." We can visualize and even analyze a single coaction between one organism and another. It is apparent, however, that it is the statistical, or summed aspect of coaction, that is significant as an integrating factor in the community. In the community this coaction is frequently inter-specific as well as intra-specific. Thus we may imagine a terrestrial region where the eating of a certain rabbit by a certain lynx is of no significance ecologically while the predation pressure of the lynx population on the rabbit population may be a coaction of considerable value in shaping the course of the entire community

(see MacLulich, 1937). In this paper then we shall view coaction as arising out of the basic biological response of aggregation. We need not stress here that aggregation in certain cases may be a closely-knit, compact phenomenon or, again, may be merely a diverse, loose-grouping of organisms (see Allee, 1931). Clements and Shelford state,

"The process of aggregation lies at the basis of social life in the biotic community, and hence it exhibits the most intimate relations with the other functions of the complex organism. It is the very essence of the association of organisms in the dynamic sense, and is primarily concerned with the integration of all the groupings, from the simplest family of plants or animals to the most highly differentiated climax. Like all community functions, it is the collective response of organisms to their environment, and in its turn it produces social patterns of all degrees of complexity" (p. 145).

It is not sufficient to label all biotic interactions as coactions and let the matter stand at that since coaction may have different end-effects on the community. Clements and Shelford have recognized three basic coactions on the basis of their effect on the coacting organisms. These are co-operation, disoperation, and competition. We shall try to differentiate briefly between these and also point out some logical fallacies in them.

Co-operation

In a philosophical sense some degree of co-operation between members of a community must be present in order that such a community can exist. This is a time-honored dictum among biologists. Darwin suggested the point in his writing and, in ecological literature, the idea goes back at least to Forbes (1887). (For a recent discussion of this point see Allee and Park, 1939). It is true that much of the co-operation is scarcely above the level of mutual toleration and equally true that most of it is merely a by-product of certain

coactions. In other words, there is co-operation in a community without the development necessarily of complex social processes to produce it. The latter, of course, may also be present in various degrees of development as the cogent syntheses of Allee (1931, 1934, 1938, 1940) have shown. In a population it would appear that many of the disadvantageous effects associated with crowding are balanced and counteracted by the advantageous effects growing out of co-operative coactions. "It is obvious that, while co-operation rests upon mutual tolerance in terms of habits and space, its positive values are derived from the conservation of energy and material, especially food, from division of labor, and from increased care, parental or nutricional." (*Bio-Ecology*, p. 150.) In considering the community as a complex social organism, co-operation becomes very important since it stresses the fact that one set of processes may bolster and implement another. This is analogous to what happens within an individual organism where many physiological processes interdigitate markedly with others. The recognition of synergism by physiologists is a case in point.

However, there are still some questions about the nature of co-operation that are left unanswered in the literature. These questions can be stated stylistically. Consider the coactions existing between two organisms, O and O'. Logically, so far as co-operation is concerned, these coactions can take the following five forms:

- (1) O and O' may both benefit from the association.
- (2) O may benefit and the effect on O' may be indifferent.
- (3) O' may benefit and the effect on O may be indifferent.
- (4) O may benefit and the effect on O' may be deleterious.
- (5) O' may benefit and the effect on O may be deleterious.

There is an element of co-operation in each of the above associations but in all but the first there are also elements of indifference, or disoperation, or competition. For example, in a predator-prey coaction one individual is the winner (predator) and another the loser (prey). Is the effect of the coaction on the predator to be called co-operation? There is need here for someone to examine critically this aspect of the co-operation concept and define it more rigorously than Clements and Shelford have done.

Our concern later will be with pointing out certain coactions in populations and showing that they result in end-effects that are co-operative or advantageous in terms of group success. At the moment we wish to suggest merely the nature of co-operation; to indicate that it arises from certain aggregate coactions within a community, and that it has value in integrating and favoring the development of that community. We wish to point out also a fact, frequently neglected by both population students and ecologists: namely, that natural selection can operate on these co-operative coactions and select *as a unit* the population. This means that selection itself frequently emerges as a factor that integrates and shapes the population. Emerson (1939a) has pointed out that selection can operate on either an intraspecific (single species) or an interspecific (mixed species) population. As an example of the latter type he states:

"Cleveland has shown that colony life is essential in the primitive termites because the symbiotic protozoa are lost at each molt and reinfestation can only occur through association with non-molting individuals. The mutual adaptive interspecific co-operation of these diverse animal populations can only be explained through the action of natural selection on the interspecific unit. Thus we find population biology merging with community ecology" (p. 296).

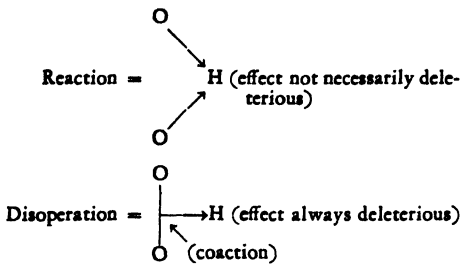
Disoperation

The aggregation of organisms within a community results in coactions that are harmful as well as beneficial (i.e. co-operative). Clements and Shelford propose to recognize those coactions that have immediately harmful effects under the term "disoperation." They say,

"... disoperation stands in direct contrast to co-operation in consequence, but it is less clearly distinguished from competition... disoperation includes chiefly those harmful effects that have to do with changed conditions or behavior, as in the accumulation of carbon dioxide, toxins or excreta" (p. 157).

It appears that disoperation must be viewed primarily as a deleterious effect impinged on the habitat; for example, the addition of poisons to the medium. If this is true how does disoperation differ from harmful reaction? This is a point not clearly treated by Clements and Shelford. I think the answer is that in many cases there is no fundamental difference between the two processes. There may be situations in a natural community where the two are distinct but frequently they must merge. Theoretically, a single organism could elaborate some toxic product and add that product to the habitat. This would be a reaction in the strict sense of the word since it does not depend on coaction between organisms. It is also possible that each member of a certain group of organisms within a community could influence its habitat completely independent of the fact that it was associated with like forms. This would also be a reaction system. However, in a typical community an important increment of the total effect would result from coactions that produce such a toxic product in considerable quantity. This would be disoperation. Possibly, there is some practical distinction between reaction and disoperation on the basis of the *rate* at which

the habitat is modified. Here, the rate might be directly proportional to the population density and thus be a function of coaction. The process of disoperation may be symbolized and contrasted with reaction by letting "H" stand for habitat and "O" for organism as follows:



Several examples of disoperation given by Clements and Shelford may be mentioned. A common disoperation among plants occurs in forests where carbon dioxide and acids are added to the soil by the population. These substances act as a barrier to invasion by certain species and may even eliminate some forms already present. They may, in other cases, permit other species to get established. Also in forests, leaves may accumulate on the floor and prevent germination of new plants. In animals, crowding frequently brings about disoperation by adding toxic excreta to the habitat. We shall make an attempt later to delineate disoperation more closely but in no case shall we urge that this factor is always recognizable in any discrete sense in the community.

COMPETITION

The last factor to be considered is competition. This, like co-operation and disoperation, also arises as a natural consequence of aggregation and is based on coaction. Clements and Shelford view competition as "... a more or less active demand in excess of the immediate supply of material or condition on the part of two

or more organisms" (p. 159). They also state, "... the essence of competition is the attempt to secure more than a proportionate share of a limited supply of something, e.g., raw materials, food, space or material for construction" (p. 157). Competition is usually most severe between organisms that have similar environmental requirements. It is not, however, limited to intra-specific coaction. There may be all degrees of competition ending in situations in communities where plants and animals are competing with each other. We shall view competition in a statistical sense as a population pressure resulting from the demand made by many organisms on a limited supply of raw material. This seems worthy of emphasis. The time is now past for thinking of competitive phenomena mainly in terms of individual battles between two organisms for an item of food, a mate, or a breeding site. Both the ecologist and the geneticist must be ready to view, and more importantly, to *analyze* competition as a selection pressure growing out of coactions that are based on group or population activity. Obviously, there will not be one competition in a community but many and the number will depend on the size and complexity of that respective community. It should also be stressed that the end-results of competition may vary according to the duration of the competitive phenomena. From a short-time viewpoint, competition can be regarded as harmful in its effects since it reduces the supply of energy and material and also decimates certain elements of the population. However, this is not true necessarily over longer periods of time since competition sets up positions of dominance and subordination and thus becomes an essential factor in community integration and succession. Over still longer time spans competition shapes selection pressures and thereby emerges as a

prime force in speciation. An interesting theoretical discussion of competition is presented by Nicholson (1933) who, so far as I can make out, views this coaction primarily in terms of food and feeding pressures. Nicholson's concepts are discussed and criticized by Thompson (1939).

A final question need be asked here: can disoperation, co-operation, and competition be clearly differentiated? The answer is *yes* in terms of formal definition but no in terms of many actual cases. We shall

cycle of cause and effect results from the interplay between habitat and its component population. This cycle is constituted by two operations; (a) action, or the influence of the habitat on the community, and (b) reaction, or the influence of the community on the habitat.

(3) In any natural community aggregation brings together a group of organisms in a habitat. These organisms exhibit collective responses that are known as coactions. These coactions constitute an-

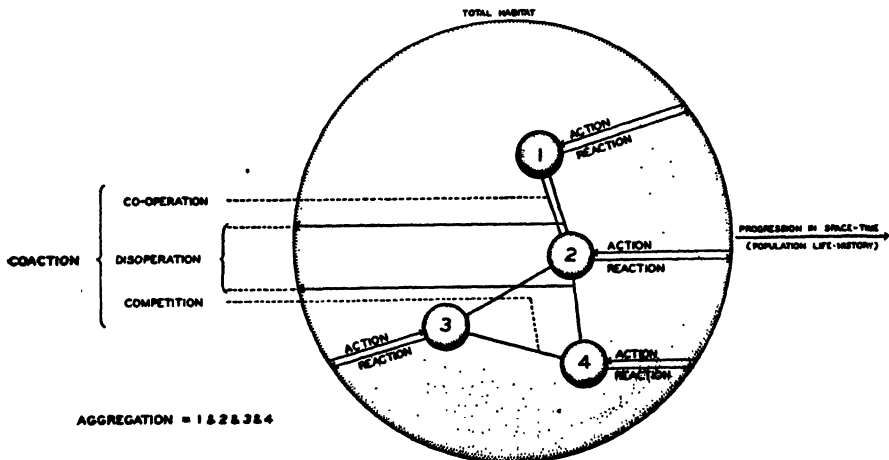


FIG. 1. SCHEMATIC REPRESENTATION OF THE ECOLOGICAL SYSTEM DISCUSSED IN THE TEXT

omit further discussion of this point until later in the paper when we are dealing with experimental material.

Summary

Before going on a brief summary of the concepts developed by Clements and Shelford is in order. The following points may be made:

(1) The authors adopt the view that the biotic community is a complex social organism. They feel that this view aids in understanding intra-community dynamics.

(2) The habitat is defined as the physical-chemical environment of the community. It has been shown that a primary

other cycle of cause and effect in the community. Coactions influence the community through (a) co-operation, which has positive value for the co-operating organisms; (b) disoperation, which has deleterious effects on the acting organisms largely through influence on the habitat; and (c) competition, which is an expression of the fact that certain coactions are directed towards exploiting an environment limited in its potentialities.

(4) The integration of a community, that is, its cause and effect relationships, is based on the continuous interoperations of the primary and coaction cycles. These cycles establish the organisms in positions

of dominance and subordination within the community. These positions are not static but are dynamic in character; they are subject to change as the primary and secondary cycles change.

It is possible that an over-simplified diagram may aid in visualizing the rôle of these factors in integrating the community. Figure 1 represents such an attempt. The figure should be thought of as a spherical model. The entire drawing represents a biotic community at any instant of time. The boundary of the sphere depicts the total habitat. Within this habitat a community has developed by aggregation. The organisms are not fixed in position but are in constant movement. They may remain relatively fixed, that is, they exhibit slight movement, for a considerable period of time. This would be the case in most climax communities where biotic balance is well established and the total population maintains essentially an equilibrium. The organisms (balls) are arranged in positions of dominance and subordination. They owe these positions to the interactions of the primary and secondary cycles within the community. The figure shows each organism related to its habitat by action and reaction. It also shows that coaction exists between all members, although all possible coactions are not drawn for the sake of simplicity, and that the coactions may result in cooperation, disoperation, or competition. By moving the model in one direction we get the analogy of change in the community in time and space (ecological succession) with patent modification of habitat and cause and effect cycles.

Critique

A word of evaluation of the Clements-Shelford system is appropriate here. It is obvious that the scheme is over-simplified and that, for many cases, one concept

merges so imperceptibly into another that the terms lose objective value. It is also obvious that there is not too much evidence among the data of ecology to test critically this system. One can easily understand the remarks of Hutchinson (1940, p. 267) who, in reviewing *Bio-Ecology*, said,

The general principles that are supposed to emerge are, however, mainly classificatory; processes occur in different communities that can be placed in a single category and designated by a single term. The general principles of ecology therefore appear as a set of rules for the construction of a language. This may be inevitable in the present state of the science; it is, however, uncertain that the language of *Bio-Ecology* will ever become a universal tongue.

It is also possible to agree with Hutchinson when he points out that the authors neglected the possibilities of statistical treatment when dealing with questions of competition and equilibrium. Despite these obvious objections the Clements-Shelford concepts do aid in classifying ecological phenomena and, more importantly, in arranging these phenomena into something of a working pattern. Doubtless with time a sounder system will be developed but to date this is the best, *in fact the only*, framework of its kind available for the use of ecologists. With this general background we wish to turn our attention now to experimental populations and see if they can be interpolated into the system of Clements and Shelford.

LABORATORY POPULATION STUDIES

Earlier in the paper it was pointed out that this effort would concern itself largely with studies made on the flour-beetle, *Tribolium confusum*, and the fruit fly, *Drosophila melanogaster*. From time to time, cases using other forms as examples will be cited but attention will center on these two. It should also be remembered that it is not our primary interest to introduce

new facts about insect populations. Rather, the interests lie in organizing and orienting a series of diverse phenomena into an ecological framework; namely, that of Clements and Shelford. Analogically, we are doing what the statistician refers to as "curve fitting." We have a hypothesis—an ecological system—and the facts—the population data—and are interested in seeing how well the two are correlated. An account of the husbandry of *Tribolium* has been published by Park (1934a, 1937a) and Good (1936). Similar material for *Drosophila* has been assembled by Morgan, Sturtevant and Bridges (1925) and Hammond (1938, 1939).

Habitat

Tribolium confusum. It is difficult to imagine a more restricted total habitat than that of this species. A bottle or dish containing some sort of pulverized grain is all that is required as far as medium is concerned; the beetles spend their entire life-cycle under such conditions. The important additional factors are temperature, preferably now below 22° or above 32°C. (Chapman and Baird, 1934), and a relative humidity ranging from 25 to 75 per cent in the experimental incubator. Holdaway (1932) has shown that flour reaches a moisture equilibrium with the humidity of the air. In most of the experimental work with *Tribolium* an effort has been made to control as precisely as possible the habitat. Thus, for a certain experiment the following constant conditions usually obtain: (1) control of volume, surface exposure, and kind of medium; (2) control of temperature (frequently maintained at 28°C.); (3) control of relative humidity (humidities of 40 to 50 per cent and 75 per cent have been used most commonly); and (4) control of light by culturing the population in absolutely dark incubators. Oxygen supply and car-

bon-dioxide accumulation do not seem to be important in the habitat of *Tribolium* since, as far as the experiments to date go, there is no evidence that these operate as limiting factors. The rate of oxygen consumption of male and female imagoes has been determined (Park, 1936) but this is a physiological datum of no immediate ecological significance.

Thus it is apparent that the habitat of *Tribolium* is easily and rather exactly definable in the terms proposed by Clements and Shelford. This habitat is more easily envisaged than that of a beech-maple climax community. The latter is a case where there are more inter-operating factors and much more variability. Both, however, are real entities that can be analyzed. There is no difficulty in applying this phase of the habitat concept to laboratory populations of *Tribolium*.

There is one complication. Clements and Shelford state, "The raw materials for food making by the plant are obviously habitat factors, but food itself is not, either for animals or hysterothytes" (p. 26). This does not seem to be true for *Tribolium*. The primary source of the beetles' food is the grain which is a major part of the habitat. There are secondary food sources based on coactions such as cannibalism. But these are of relatively slightly nutritional importance in terms of the complete population. Therefore, it will be necessary to include food supply as a habitat factor when dealing with the *Tribolium* studies. I am not sure this really transgresses the definition. In a natural terrestrial community many subterranean forms, as annelid and nematode worms, get their nutriment from organic material dispersed throughout the soil. In this case soil is a habitat factor in much the same way as flour for *Tribolium*. Also, certain termites and the

roach *Cryptocercus*, eat wood directly and obtain starches and sugars by means of the symbiotic activity of intestinal flagellates. In this case a log or a tree is an important part of the habitat. Unless I have misinterpreted Clements and Shelford, it seems possible to retain their concept of habitat and still have it apply in certain cases to food supply. It is now experimentally feasible to split the habitat of *Tribolium* so that the food elements can be separated from inert physical medium and substratum. A recent abstract (Park and Burrows, 1939) called attention to a synthetic medium in which *Tribolium* could be cultured. In this medium a finely powdered wood dust formed the non-nutritive base and certain substances (casein, dextrose, Osborn-Mendel salt mixture, and yeast) added to the wood served as the food supply. This synthetic medium is a habitat in the same sense as grain but it can be broken down chemically more readily than can flour.

Drosophila melanogaster. The habitat of *Drosophila* reared under experimental conditions offers certain complications not present for *Tribolium*. The fruit fly is cultured in a more atypical environment than the flour beetle. While the latter genus undoubtedly arose as an under-bark form (Good, 1936) it is largely confined at present to flour and cereal products. Thus a container of flour if large enough is a quite natural habitat for *Tribolium*. *Drosophila melanogaster* probably arose as a tropical and subtropical form correlated in its distribution with fruit. The laboratory habitat of *Drosophila* therefore departs more from a natural habitat than is the case for the beetle. In one sense an analysis of a *Drosophila* habitat is simpler than for *Tribolium*. The former feeds apparently on yeast mycelia (Morgan, Sturtevant and Bridges, 1925; Hammond, 1938-1939) that grow on a nutritive base.

This means that the feeding mechanisms of the fly population are coactions similar in principle to those developed for field communities by Clements and Shelford. Here, the habitat can be separated partly from food although *Drosophila* also probably utilize agar medium to some extent as nutriment.

Since most of the population work with *Drosophila melanogaster* has come from the laboratory of Raymond Pearl we shall stress the habitat used by that group. From our viewpoint the total habitat can be broken down into four units: air volume in the container above the medium; the exposed surface of the medium; the medium proper; and the experimental conditions maintained in laboratory incubators. Later it will be shown that all these factors are important, in one way or another, in our ecological system. Suffice it to say here that (1) the medium furnishes a physical substratum in which the larvae burrow and develop; (2) the surface of the medium furnishes a niche for the growth of yeast, feeding of the flies, copulation and associated behavior responses and oviposition; (3) the air volume within the bottle is an area for flight; and (4) the entire bottle can be maintained in an incubator under constant conditions of temperature, humidity, and light. As was the case for *Tribolium*, oxygen deficit and carbon dioxide accumulation normally do not appear to be limiting factors. The medium used (Pearl and Penniman, 1926) is a synthetic composition of agar plus certain salts with the pH regulated. This medium ("S-101") has the virtue of reproducibility and considerable constancy and, while it probably does not yield as large populations as the typical cornmeal-molasses of geneticists, it is easier to standardize and, due to its transparency, it permits fecundity counts to be made.

Action

Action has already been defined and illustrated as the effect of habitat on the community. In this section several examples of action as it occurs in *Tribolium* and *Drosophila* populations will be discussed.

TABLE 1

Duration of egg, larval and pupal stages of *Tribolium confusum* at 22°C. and 32°C.

(Data of Chapman and Baird, 1934.)

STAGE	TEMPERATURE (centigrade)	MEAN DURATION (days)	COEFFICIENT OF VARIABILITY (per cent)
Egg	22	14.09 $\pm$ 0.17	1.7
	32	4.41 $\pm$ 0.09	3.0
Larval	22	61.10 $\pm$ 3.27	8.0
	32	17.35 $\pm$ 0.52	4.3
Pupal	22	17.86 $\pm$ 0.59	5.2
	32	5.37 $\pm$ 0.48	13.1

TABLE 2

Rate of oviposition of *Tribolium confusum* females coloured at 22°C. and 32°C. for 13 days

(Data of Chapman and Baird, 1934.)

TEMPERATURE	MEAN EGGS PER FEMALE PER DAY	COEFFICIENT OF VARIABILITY (per cent)
22	1.898* $\pm$ 0.797	62.2
32	10.729 $\pm$ 1.948	26.9

* Mean less than 3 times its probable error.

Tribolium. Temperature and humidity are two habitat factors that have been worked on for *Tribolium*. Chapman and Baird (1934) kept populations at temperatures of 17°, 27°, and 32°C., and measured the effect of these temperatures on (1) duration of the egg, larval, and pupal stages and (2) rate of oviposition. Their results are summarized in abbreviated form in Tables 1 and 2. These data are straight-forward and, from a physiological viewpoint, commonplace. They show

that the rate of metamorphosis is more than tripled by a ten degree rise in temperature and that fecundity performance at 32° is nearly six-fold that at 22°. From the point of view of this paper the data are instructive in that they furnish a diagrammatic example of action: namely that temperature, a habitat factor, acts on a population and increases its rate of development and reproduction. Obviously, these two responses are of the greatest importance in population growth. It is apparent then that temperature must be viewed as a highly significant habitat factor. In most of the studies to be discussed the rôle of temperature will be ruled out. This is an experimental simplification only and does not mean that this factor can be neglected in any complete population analysis of *Tribolium*.

Most action elicits some of its effects on the population through coaction. Temperature is probably as pure an example of uncomplicated action as any case that could be found. A stimulus, temperature, is presented and the population responds in terms of rate effects. These rates are primarily controlled by temperature *per se*; that is, by the specific action of this habitat factor on the physiology of the individuals comprising the population. In the case of most habitat influence the cause and effect cycle is more circuitous as we shall see. Further examples of temperature as a habitat factor for *Tribolium* can be found in the following: Chapman, 1931; Dick, 1937; Good, 1936; Nagel and Shepard, 1934; Oosthuizen, 1935; Park, 1934a, 1935a. A good discussion of temperature coefficients applied to insect oviposition appears in the paper of Harries (1939).

An interesting case of habitat action on *Tribolium* populations is reported by Holdaway (1932). In this investigation beetles were reared under relative humid-

ities of 25, 50 and 75 per cent. It was shown that humidity effects varied with the metamorphic stages. Thus

"... viability of the eggs and pupae is at a maximum at low humidities, while for larvae it is at a minimum. As regards the duration of the various stages there is little effect on eggs and pupae. . . . The larval stage is the one in which duration is most affected by atmospheric moisture. It increases with decrease in humidity" (pp. 296-297).

These results are clear-cut illustrations of habitat action. They show that certain beetle stages have their developmental optima at certain humidities. In this respect the data are similar to those actions described for temperature. However, there is a further complication. Holdaway showed that the total population attained its greatest size when cultured at 75 per cent relative humidity. In part this is an expression of an interesting coaction elicited by the action of humidity. Ford (1937, p. 4) summarizes these findings as follows:

"Of particular importance, however, in relation to the size of the balanced population is the eating of eggs and pupae. Holdaway suggests that the feeding stages of *Tribolium*, i.e., larvae and adults, may utilize the non-feeding stages, i.e., eggs and pupae as sources of moisture. This might account for the increase in size of the asymptotic populations with increasing humidity; for at 75 per cent relative humidity the flour itself contains more moisture than at 25 per cent relative humidity, and consequently there is less need for larvae and adults to feed on eggs and pupae, and therefore a greater survival of these stages."

Holdaway himself concludes

"It can then be affirmed that the mechanism by which atmospheric moisture regulates *Tribolium* populations is an alteration in intensity of the normal biotic control which this species can exert on itself; or in other words, the effect of the physical factor humidity, on the insect population is *per medium* of a biotic effect, the intensity of which is regulated by the physical effect of atmospheric moisture on the moisture content of the flour." (P. 298.)

In this connection the paper of Voûte (1938) should be consulted.

From our viewpoint this action system can be summarized as follows: (1) the habitat factor is humidity; (2) humidity has end effects on both the component stages of the population (eggs, larvae, pupae, and imagoes) and the equilibrium point of the total population; and (3) the action of humidity is in some cases direct; that is, a specific humidity effect on the physiology of a certain stage, and indirect in others; that is, operating by altering coaction.

Drosophila. Temperature is an important factor for *Drosophila* populations as well as for *Tribolium*. Its action can be illustrated by summarizing briefly some of the effects of temperature changes on oviposition, metamorphosis, longevity, and body size.

Oviposition. An interesting analysis of the effect of temperature on fecundity appears in the work of Alpatov (1932). This author wanted to see if the temperature at which *Drosophila melanogaster* was reared (i.e. the metamorphic period) would have any effect on the oviposition of the flies as adults. To get at this he cultured one group of fly populations at 18°C., and another group at 30°C. As soon as these flies emerged they were all placed in a constant temperature of 25°C., and their life duration, total egg production, and rate of egg production per day were assayed. Alpatov's data are summarized in abbreviated form in Table 3. This table shows that (1) flies bred at 18° produced more eggs than flies bred at 30° even though the temperature at which the imagoes were kept was the same, 25° in both cases, and (2) the 18° females lived significantly longer than the 30° females. This is a case of a "deferred" habitat action. Temperature acts on the larvae and the effect of this can be detected later in

fecundity performance and longevity. Alpatov thinks that the larvae develop so rapidly at 30° that they emerged in an undernourished condition as imagoes. It is possible that, in addition to the action of temperature in increasing the rate of metamorphosis, food competition between the larvae of the 30° populations is intensified. Again this may be a case where a habitat action is the primary influence with a subsequent coaction the secondary influence.

TABLE 3

Oviposition of *Drosophila* females reared at 30°C., and 19°C., and kept as imagoes at 25°C.

(Data of Alpatov, 1932.)

TEMPERATURE OF DEVELOPMENT TEMPERATURE OF IMAGINAL LIFE (degree C.)	TOTAL NUMBER OF EGGS	EGGS PER DAY	FEMALE DURA- TION OF LIFE (days)
30 25	430.3 ± 33.4	14.84	31.58 ± 1.74
19 25	941.1 ± 35.9	26.28	39.05 ± 1.63

Another case where temperature has been shown to affect oviposition is reported by Dobzhansky (1935) for *Drosophila pseudoobscura*. This author described for this species two physiological races, A and B, that appeared alike anatomically but were not interfertile. He found race A was normally an inhabitant of areas where the climate was warm and variable while race B lived in damp, cooler areas. Dobzhansky demonstrated that race A females produced more eggs than race B females when their fecundity was assayed at 25° and 27.5°. However, race B females produced more eggs than A at 9°,

14°, and 19°C. This is an interesting example of the action of an experimental habitat because of its obvious connection with habitat factors obtaining in the field.

Metamorphosis. One of the earlier analyses of the action of temperature on the duration of the larval and pupal stages of *Drosophila* was that of Loeb and Northrup (1917). Their data are summarized in Table 4 where it is shown that both larval and pupal development is accelerated by increased temperature within the range reported. These results are quite similar to those summarized already for

TABLE 4

Duration of life of *Drosophila* reared aseptically in various temperatures

(Data of Loeb and Northrop, 1917.)

STAGE	MEAN DURATION OF LIFE (days)				
	15°C.	20°C.	25°C.	27.5°C.	30°C.
Larval.....	17.8	7.77	5.82	4.15	4.12
Pupal.....	13.7	6.33	4.23	3.20	3.43

Tribolium except that in this case the flies were cultured under aseptic conditions free from micro-organism contamination. Another analysis of temperature and metamorphosis is reported by Hammond (1938-1939) in discussing the work of Bonnier (1926).

"Bonnier, using a sex-linked mutant, yellow stock, observed his culture bottles every two hours and removed each pupa formed during the preceding period to a separate bottle and later observed these bottles every two hours while the imagoes were emerging. His results were as follows: high temperature speeded up development in both larval and pupal periods. At 30° the females developed significantly faster than the males in both the larval and the pupal stages. At 25° the pupal period was significantly shorter for the males than for the females (difference 4.1 hours), but there was no significant difference in the larval period." (P. 40).

Longevity. There is a good deal of evidence to show that temperature may influence a *Drosophila* population by its action on life duration. This is an important case to include in a discussion of habitat action since the significance of mortality from the population viewpoint hardly can be overstressed. A summary of many such cases is given by Pearl (1928) and some interesting ecological interpretations are suggested by Bodenheimer (1938). A specific illustration is in order. Alpatov and Pearl (1929) reared flies at 18° and 28°C., and as the flies emerged they were placed in popula-

ened duration of imaginal life which we observe. In the 28°C. flies there is a short developmental period and a consequent *rapid rate* of energy expenditure during growth and during imaginal life (flies very active). This leads to the expectation of a short duration of imaginal life, which is in fact observed." (P. 65.)

This is another case where the habitat factor, temperature, plays its primary rôle by altering certain physiological velocities associated with mortality.

Body size (imagos). The final habitat action we shall discuss here is the influence of temperature on body size. In the study just reported (Alpatov and Pearl, 1929) the effect of temperature on femur length, tibia length, wing length, and wing breadth of *Drosophila*, as well as on longevity, was analyzed. It was shown that flies developing at 18° are larger than those developing at 28° in respect of all four measurements. Alpatov (1932) showed that both the length and breadth measurements of the wings of wild-type *Drosophila* were smaller if the larvae were underfed or reared at high temperature. Harnly (1930) reported somewhat different results for vestigial *Drosophila* males. Hammond (1939, p. 47) summarizes these data as follows: "... in vestigial males a rise in temperature from 18.3°C. to 29.0°C. produced a very slight *lengthening* of the wings; between 29°C. and 30°C. the wings increase 25 per cent in length, and from 30° to 31°C. they increase 70 per cent in length."

Before concluding this discussion of action a word of caution is necessary. The reader should not get the impression that temperature and relative humidity are the only habitat factors known for experimental populations, or for that matter and quite obviously, for natural populations. We have stressed these two cases for illustrative purposes. They provide good examples of the actions they

TABLE 5

Effect of temperature of metamorphic period and imaginal period on life-duration of Drosophila
(Data of Alpatov and Pearl, 1929.)

TEMPERATURE DURING IMAGINAL LIFE (centigrade)	PERCENTAGE WHICH DIFFERENCE BETWEEN FLIES REARED AT 18°C. AND 25°C. IS OF 18° FLIES	
	Males	Females
18°	19.5	7.6
25°	16.1	12.7
28°	—	7.0
Mean	17.8	10.2

tions maintained at 18°, 25°, and 28°. Thus there were two temperature series during post-embryonic development and three series during imaginal life. The data are summarized in Table 5 where it is shown that flies that had metamorphosed at 18° always lived longer, as a population, than flies reared at 28°. This is true for both males and females although the latter are more longevous in all series. The authors interpret their results as follows:

"... the effect of increased temperature is to speed up the *rate* of the biological processes involved. In the 18°C. flies we have a *slow rate* of energy expenditure in growth and during imaginal life (flies very inactive), and we should therefore expect ... the length-

depict and are probably as direct and uncomplicated as any that could be found. We shall not forget the important rôle of habitat action in passing on to consider other factors; rather, it will be our hope to continually relate it to the general ecological system of Clements and Shelford. We shall particularly stress action as a corollary of reaction in the next section.

Reaction

Reaction has been defined and discussed as the effect of the community on the habitat. It has been shown that actions and reactions go on continuously within any biological grouping and that they constitute the primary cycle of cause and effect. At this place we wish to illustrate reaction as it exists in laboratory populations. This means that cases must be found where it can be demonstrated that the population impinges an effect or reaction upon the habitat or physical-chemical environment.

Tribolium. For *Tribolium* there are a number of reactions that are immediately obvious. For, example, the beetles tunnel through the medium thus altering its topography and comminute the particles of flour and meal by the grinding action of their mouthparts. However, these are somewhat in the category of less important effects. We wish to examine here a more complex reaction system that can be shown of significance in controlling the integration and growth of the entire population. I have been interested for some time in analyzing a *Tribolium* population problem that I have called the "conditioned flour problem." A series of papers on this subject have appeared (see Park, 1934, 1935, 1936, 1936a, 1937, 1938, 1938a, 1939; Park and Woollcott, 1937; Park, Miller and Lutherman, 1939; Stanley, 1934; Ford, 1937). The present report is

not concerned with reviewing in any detail these studies but, rather, will attempt to show that this problem in its broader aspects has application to the ecological system under analysis. This application must be made in several places in the paper; it cannot be disposed of under the heading of reaction alone. However, there are enough phases of reaction inherent in the conditioning work to warrant its introduction here.

A brief background is in order. Conditioning illustrates a population effect operating primarily through alteration of the habitat. If *Tribolium* populations are allowed to age without experimental disturbance of the flour in which they live they gradually become extinct and the flour noticeably changes in chemical and physical composition. This change in the medium is spoken of as biological conditioning. "Conditioned flour" thus is a substance which is produced by the beetles in their normal course of living. It is an inevitable product of *population activity* owing its existence entirely to the cumulative effects of the breeding and general behavior of the beetles themselves. More specifically, conditioned flour differs from fresh or unconditioned flour in that the beetles inhabiting it have reduced its nutritive value through constant feeding and have added certain by-products such as excretory wastes and frass not present in the original medium.

Several points are immediately apparent. First, the processes just described as occurring during conditioning are obviously not all reactions. Second, conditioning is of no real significance unless it affects in turn the development of the population. These points merit examination. It has been shown that a *Tribolium* population alters through its own activity the habitat by reducing the nutritive level and adding certain by-products to the

medium. What ecological processes are concerned with this conditioning? I think it can be safely said that action, reaction, and certain coactions are all functional. A question immediately arises: shall the alteration of the flour (habitat) caused by conditioning be called reaction or disoperation? It is reaction in the sense that the population has modified the habitat; disoperation in the sense that through coactions an effect is produced on the habitat that is deleterious in terms of the total population. There are also a series of definite actions since conditioned flour, whether produced by reaction or disoperation or both, affects markedly the development and reproduction of the beetles. There is risk here in getting bogged down in the terminology without accomplishing anything constructive. This is done too frequently in ecological writing and certainly should be avoided in this paper. For purposes of expediency, let us assume temporarily that conditioning illustrates reaction and proceed from that point.

In terms of the population it is meaningful to examine conditioning as an environmental factor that initiates action. The position is this: we know that conditioned flour is a population product; we know something, though far from all, of its nature; how does this biotically altered medium affect the physiology of *Tribolium* and thereby the development of the population? This seems a logical approach since it facilitates the analysis of the primary cycle of cause and effect, action-reaction, under one treatment.

Following are some of the actions of conditioned flour on the physiology of *Tribolium* (Park and Woolcott, 1937):

(1) It reduces their cannibalism (i.e. the rate at which imaginal beetles eat their own eggs) to about half that of control beetles living in fresh flour. This is an

example of an action (conditioning acting on the beetles) followed by a reduction in competition for eggs (i.e. lowering of the rate of egg consumption).

(2) It reduces their fecundity drastically—lowering it three or more times below a control level by reintroduction of the beetles into fresh or unconditioned flour. It also reduces the fecundity of virgin (i.e. non - fecundated) female beetles. These are probably cases where conditioning acts directly on the beetles with no important secondary coactions.

(3) There is some evidence that conditioning affects fecundity through the males as well as through the females since in one group of experiments the data showed that females reared in fresh flour when mated with males reared in conditioned flour had a lower rate of reproduction than did control (fresh) males mated to control females. In this case the action appears to be first on the male reducing in some way his sexual efficiency. The male's effect on the female represents some form of coaction.

(4) Conditioning increases the relative variability of *Tribolium* fecundity. This is probably another case of uncomplicated habitat action working directly on the physiology of the ovipositing female.

(5) Conditioning apparently does not alter in any consistent pattern the fertility of the eggs. In other words, once produced, eggs from conditioned-flour beetles have about as good a chance of hatching as do eggs from fresh-flour beetles. This is another way of saying that, while the conditioned flour markedly lowers egg fecundity, it has no action on egg hatchability. Thus, reproductive effects in the population caused by conditioning are fecundity rather than fertility effects.

(6) It increases the duration, variability, and mortality of larval metamor-

phosis. There is evidence that the major factor in this case is the direct action of conditioned flour on the larvae. Competitive coactions, other than those involved in actually conditioning the flour, appear unimportant. It has been shown (Park, 1938; Park, Miller and Lutherman, 1939) that if the larvae are cultured in dense populations with the flour experimentally kept from getting conditioned no lengthening of the larval period or increase in larval mortality is observable. In this case there would be many coactions in the crowded cultures but they would be essentially unimportant in causing the type of metamorphosis effects observed for conditioned populations.

A final question is this: what is the summed effect of these actions on the development of the total population? The answer is clear for two reasons: first, all described conditioning effects are either indifferent (fertility) or deleterious (fecundity reduction, lowered rate of metamorphosis, increased larval mortality), and second, the medium is conditioned in direct proportion to the age of the culture. This means that populations of *Tribolium* will gradually decline and eventually become extinct due to the accumulation of conditioned flour and the action of this flour on the beetles' physiology.

In summary, it can be repeated that (1) conditioned flour is a habitat modified by the reaction and disoperative effects of the total *Tribolium* population; (2) this habitat has certain known actions on the population and its constituents that lower the beetles' productivity and developmental efficiency; and (3) conditioning, working through these physiological processes, brings about the decline and eventual extinction of the population. We shall return to selected aspects of the conditioned flour problem later. It seems unnecessary to labor the point that this

analysis based on laboratory research has direct application to natural communities when interpreted in the light of the Clements-Shelford concepts. Though simplified, laboratory populations are total communities.

Drosophila. *Drosophila* population studies have concerned themselves largely with coactions. This will be discussed later. There are no analyses to my knowledge that can be used as illustrations of reaction. A few possible reactions can be imagined but their significance, if any, has not been tested experimentally. An obvious case is the burrowing of the maggots in their substratum. This is probably a reaction of some importance since *Drosophila* larvae must develop in a moist habitat such as that provided by tunnels in the agar. It is also possible that the fly population reacts on its environment in some way analogous to conditioning in *Tribolium*. This is a fertile field still open for attack and its importance is suggested by a statement of Bodenheimer (1938). This author is concerned with the growth of a total population of a Palestine strain of *Drosophila*. He divides this growth into three periods: Period of Initial Growth (0-9 days); Period of Rapid Growth (10-14 days); Period of Oscillations (15-22 days); and Period of Contraction (23-35 days). In discussing the last phase Bodenheimer says,

"The final contraction [of the population] is therefore not due to the intra-specific struggle for existence [coaction], but some intoxication, especially effective in the adult stage. The enormous mortality following hatching of new flies during the latter part of this period before the end of their first day of adult life points to this direction. Population pressure is certainly not involved in this adult mortality, or only to an inconsiderable extent. More detailed studies are needed before any explanation may be given. The form of decrease agrees with that of a moderate intoxication curve" (p. 76).

It is probable that this "intoxication" effect will prove to be a potent action-reaction or disoperative system when finally analyzed. It is hoped that this analysis will be forthcoming soon.

Tenebrio. Michal (1931) reported that a population of meal-worms (*Tenebrio* larvae) raise the temperature and humidity of their medium. This is a diagrammatic illustration of reaction—the population modifies the physical-chemical habitat to a noticeable degree.

One reason for working with experimental populations lies in the fact that frequently they permit refinements to be made in the analysis of environmental relations that can only be approximated in the field. Typically, in dealing with natural populations one can merely name a process, say, as an action or reaction without understanding its various degrees of complexity. This complexity may build up with time as both the habitat and the population change. The older

population still has internal phenomena that properly are actions and reactions but they are different and usually more intricate. These "higher order" factors can be studied and experimentally dissected. In this point lies one of the merits of the laboratory population as an ecological tool. An example will make the point. We conclude that conditioned flour is a product of reaction and disoperation and that, through these mechanisms, a modified habitat results. This habitat acts back on the population with definite end-results. The cycle is not completed here, however, for as the culture matures, coactions as well as reactions increase in intensity and in type and the habitat suffers further modification. And so the story goes. In many cases this chain of events can be analyzed in the laboratory better than it can in the field.

(To be concluded)



COMPARATIVE ANATOMY AND PHYSIOLOGY OF THE ANTERIOR PITUITARY

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INTRODUCTION

TOPOGRAPHICALLY, the pituitary gland occupies one of the most protected positions in the vertebrate organism. In the evolution of species, however, it would seem that a structure concerned with so many vitally important physiological processes must be subject to severe phylogenetic "stresses." In some instances new "target organs" have been brought under the sphere of influence of the pituitary (e.g. the mammary glands) or old ones have virtually disappeared (e.g. melanophores in adult birds and mammals). Furthermore, in some instances evolution has wrought an extreme anatomical or functional change in one of the pituitary "target organs." This is the case with the pliable vertebrate genital system. The appearance of corpora lutea in reptiles and mammals, the suppression of yolk deposition in the maturing egg, the progression from oviparity to ovoviviparity and viviparity, and the differentiation of types of protein metabolism according to the kind of egg laid (cleidoic or non-cleidoic)—all of these may be reflections of qualitative or quantitative changes in hypophyseal secretions. Frequently, even within relatively small animal groups, the target organ has been shown to vary between species in the temporal spacing of its periods of func-

tional activity and rest. Have there been corresponding changes in the pituitary? To the comparative physiologist the changes in the relationship between the pituitary and the structures influenced by its secretions present an absorbing, and as yet an incompletely understood problem.

Morphological studies of the pituitaries of many vertebrates have been in progress for some time, and some especially thorough work has been done in the mammals and birds. Unfortunately, most of this work has been primarily exploratory, and the summarized data allow generalizations only in regard to the more gross features of hypophyseal anatomy. Work with fish, amphibia, and reptiles does not yet provide an adequate basis for a functional interpretation of observed morphological features. There is even less justification at the present time for declaring the functional equivalence of certain parts of the pituitary in different lower vertebrates.

In all vertebrates the pituitary is formed by the union of a lobe of the floor of the brain with a lobe or vesicle of somatic ectoderm, which migrates inward from the oral epithelium or (in cyclostomes) from the ectoderm of the upper lip. The lobe of somatic ectoderm then becomes further differentiated into an intermediate, or juxta-neural region (secondarily lacking in birds), and an "anterior" or distal

part. In many animals there is also differentiated a pars tuberalis, which is situated dorso-laterally in respect to the rest of the gland and is most often applied to the infundibular stalk. In teleosts and cyclostomes Stendell (1913) named a region between the pars intermedia and pars distalis, the *Übergangsteil*. The problem of the functional and anatomical status of the *Übergangsteil* has provoked considerable discussion, but its solution awaits physiological experimentation. In elasmobranchs, pituitary structure reaches its greatest apparent complexity with the addition of a "ventral lobe" extending ventrad from the base of the pars distalis. The nature of this lobe as is the case with some other parts of the elasmobranch pituitary, is not clear.

Pituitary homologues in the invertebrates

In the most primitive of living vertebrates, the cyclostomes, there is, according to Tilney (1937), already a well-developed pituitary consisting of pars nervosa, pars intermedia, pars tuberalis, *Übergangsteil*, and pars distalis. It is difficult to conceive how this organ, having such diverse anatomical and physiological properties, can have had its sudden inception in the vertebrates. It seems probable that the pituitary gland as we know it is the product of a considerable, and still wholly unknown, evolutionary history. Many have attempted to find structures comparable to the pituitary in the lower chordates, in the arthropods, and in the echinoderms, each of which is believed by some zoologists to bear an evolutionary relation to the vertebrates.

Perhaps the most reasonable suggested invertebrate homologue is the subneural gland of urochordates, which has been described by early workers as an excretory organ. This homology has had such distinguished promulgators as Éd. van

Beneden (1884) and W. Bateson (1886). In these animals the gland, which is usually median, but may be bilateral, is most often located ventral to the ganglionic "brain" and communicates through a ciliated duct with the posterior part of the mouth (Delage and Hérourard, 1898). The urochordates are so degenerate, and have so unusual a developmental history, that it is difficult to evaluate this suggestion on the basis of the few anatomical similarities seen between the subneural gland and the vertebrate pituitary. However, the discovery that extracts of subneural glands have pressor and oxytocic activity, and melanophore-dilating action in frogs seems highly significant (Bacq and Florkin, 1935). Hogg (1937) declares that he has produced mild ovarian stimulation in mice with extracts of ascidian (*Polycarpa tecta*) subneural gland. Benazzi (1939) could not confirm this finding in tests in which he administered as many as 200 *Ciona intestinalis* subneural glands to young rats, or 450 glands to an adult female salamander, *Triton cristatus*. On considerably less evidence various structures in other protochordates have been suggested as homologues of the vertebrate pituitary. In the Hemichordata three different organs have been indicated, on morphological grounds, as related to the pituitary: (1) the proboscis pore, a dorsal opening of the coelomic cavity within the proboscis (Bateson, 1886; Willey, 1899), (2) the notochord, an anterior evagination from the mouth into the proboscis (Harmer, 1897; Masterman, 1899), and (3) the preoral ciliary organ, a crescentic band of ciliated cells on the posterior surface of the proboscis (Brambell and Cole, 1939). In these animals the homology is therefore far from clear. On similar grounds the preoral pit (Bateson, 1886) or the preoral pit plus the olfactory pit (Willey, 1899) represent the

hypophyseal homologues in Cephalochordata (*Amphioxus*). Even the anterior nephridial tubes (Legros, 1909) and the taste buds (Tretjakoff, 1929) of *Amphioxus* have been involved in this fertile speculative field. The eye-stalk of the crustacea, from which may be extracted a melanophore-dilating hormone (Abramowitz, 1937) and a hormone causing accumulation of water in frogs (Gray and Ford, 1940), and the corpora allata of insects which seem to have a gonadotropic effect in insects (Pfeiffer, 1939) have been shown to have pituitary-like functions, but their homology is extremely questionable. At any rate it remains to further work to determine whether the occurrence of chromatophorotropic substances in eye-stalk and subneural gland extracts, is of any greater significance from the point of view of homology than the finding of sex hormones in non-homologous organs in invertebrates, or in plants.

Comparative gross morphology of the pituitary

The recent careful work of Tilney (1937) on the pituitary of *Petromyzon* has definitely established its complex nature in the lampreys. The large "hypophyseal canal" which is still described in recent textbooks (1939) has been declared by Tilney to be an artefact, and not the primitive "anterior lobe." No suitable study making use of improved modern techniques has ever been made of the hypophysis of the hagfish, the only other type of living cyclostome. Both Stendell (1913) and De Beer (1926) have made the interesting claim that the pituitary in hagfishes consists of no more than a number of patches of undifferentiated cells beneath the infundibulum. It is surprising that this claim, which would establish the hagfish pituitary as different from that in the entire class Vertebrata, has not stimulated further investigation.

In some recent preliminary work with the Pacific coastal hagfish, *Polistotrema* (*Bdellostoma*) *stouti* the writer has been able to confirm, in general, the statements of Stendell and De Beer. Study of the skeleton of the extinct primitive cyclostomes, the cephalaspid ostracoderms, has revealed a median pore on the dorsal side of the head, which Patten (1912), Stensiö (1927), and others call the "hypophyseal pit." If this identification is correct, then the extrabuccal derivation of the epithelial hypophyseal lobe in cyclostomes may be assumed to have had an early origin, and might be the primitive mode of origin for all vertebrates. Embryological studies in amphibia in which the hypophyseal anlage may be traced from an originally dorsal to a finally ventral position make such a mode of origin easily explicable.

It may be concluded from Tilney's studies that the common Ordovician ancestor of the Cyclostomata and the higher fishes must have had an organized pituitary. In the light of existing information it seems highly improbable that a satisfactorily complete history of the organization of the anatomical and physiological pituitary complexes will ever become available.

The changes of the pituitary within the class Pisces have been even more diverse than those within the entire group of higher vertebrates. The pituitary of elasmobranchs is entirely unlike that of other fish. In fact it resembles the gland of higher vertebrates even less than does the pituitary of *Petromyzon*. However, within the elasmobranch group the hypophysis is quite uniform and Norris (1936) who made a study of 72 species, found that certain minor differences were correlated with taxonomic groupings. Two main types of elasmobranch pituitary could be distinguished, a selachoid (shark) and

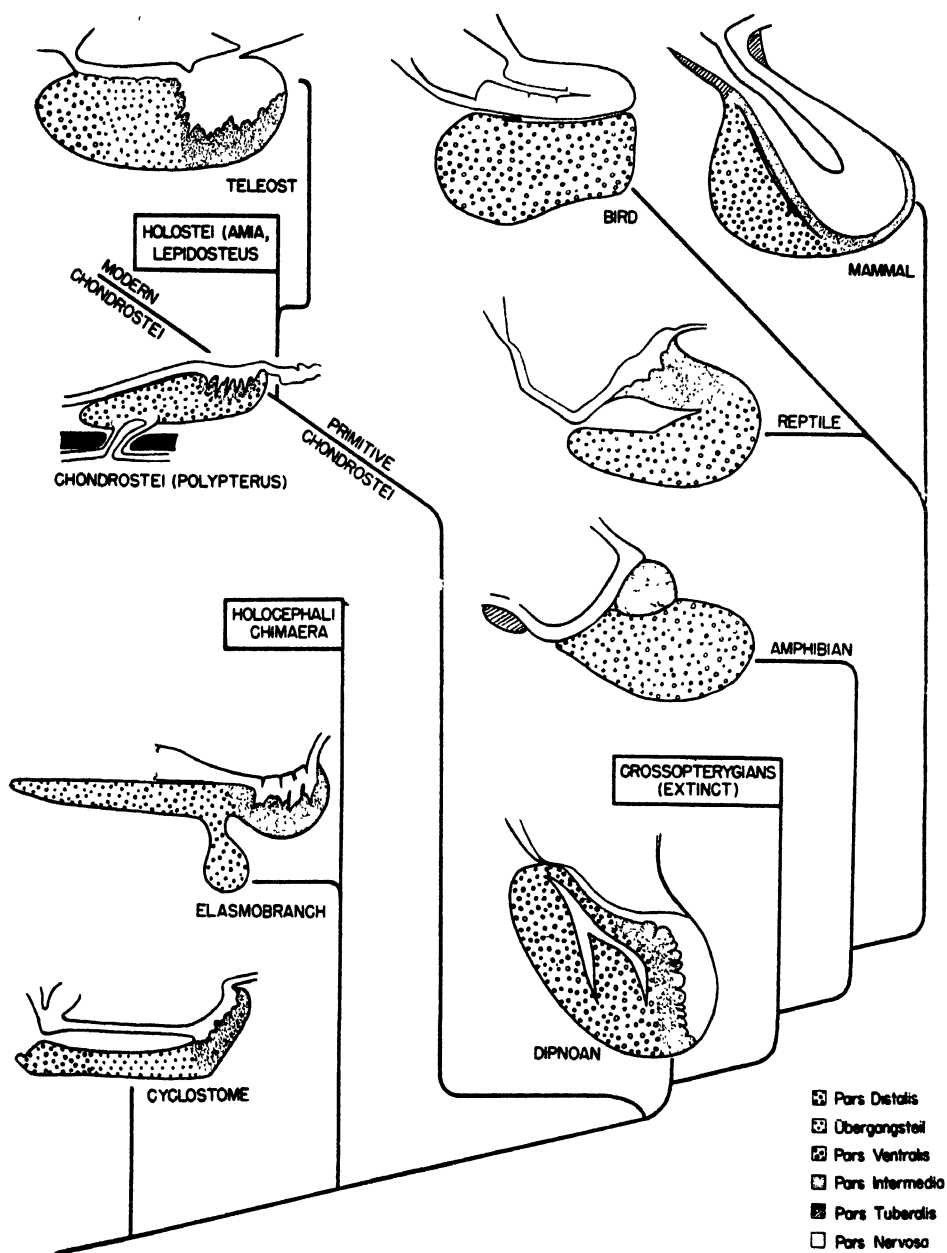


FIG. 1. PHYLOGENESIS OF THE VERTEBRATE PITUITARY

All drawings are schematic diagrams, not intended to accurately represent any single species. Drawing of dipnoan based on Griffiths (1938). Drawing of cyclostome based on Tilney (1937).

a batoid (ray) type. The diplospondylous, cyclospondylous, and asterospondylous sharks in turn each displayed a distinctive hypophyseal organization. No study has ever been made of the pituitary of Holocephali (e. g. *Chimaera*) which left the main vertebrate line approximately at the same time as the elasmobranchs but soon diverged from them to follow an independent developmental course. A knowledge of the holocephalian pituitary may make possible a better understanding of this organ in the elasmobranchs. (See Fig. 1.)

Slightly higher in the vertebrate line are the dipnoans (lung-fishes) and crossopterygians—fish which gave rise to the primitive tetrapods. The crossopterygians are now considered extinct. The living representatives of the Dipnoi seem to possess only the three hypophyseal lobes found in higher vertebrates (De Beer, 1926; Griffiths, 1938).

The Actinopterygii, or ray-finned fishes, diverged from the vertebrate line at a point similar to the dipnoans and crossopterygians and are today the dominant type among the fishes. The most primitive actinopterygians, the Chondrostei, (*Polypterus*, sturgeons), gave rise to the Holostei (*Amia*, *Lepidosteus*) which were intermediate in the final development of the very numerous Teleostei. In *Polypterus* and *Calamoichthys*, chondrosteans which have been characterized by Romer (1933) as being "in many features the most primitive of living bony fishes," the anterior lobe presents a peculiar feature—a direct connection with the buccal epithelium (Bickford, 1895; Gerard and Cordier, 1936). In *Polypterus* this connection is a short hollow stalk opening directly into the mouth cavity and displaying at its upper end a transitional zone of cells from the epithelial to the hypophyseal type. The position of this stalk suggests a comparison with the

ventral lobe of elasmobranchs. No study complete enough for comparative purposes has yet been made of the pituitary in adult Holostei. De Beer (1923) has described an extra-buccal origin of the hypophyseal anlage in embryonic *Amia*. Tilney (1911) has published a very brief and inadequately illustrated account of the pituitary of *Lepidosteus*. In this description it appears that a basophilic zone exists anterior to the pars intermedia which may be comparable to the teleost *Übergangsteil*.

The Teleostei present the distinctive hypophyseal structure, the *Übergangsteil*. Tilney (1937) has compared the cortical region of the pars distalis of the *Petromyzon* hypophysis to the *Übergangsteil* of teleosts but the validity of this comparison may be questioned. Bock (1928) and Scruggs (1939) are inclined to regard the *Übergangsteil* as a structure peculiar to the teleosts and having no homologue in other vertebrates. Such statements cannot be tested until it is possible to determine the physiological value of these regions by experimental procedures. The teleost pituitary has received considerable attention but it is a commentary on the criteria now used for identification of hypophyseal regions in teleost fishes, that even recent workers cannot agree on basic matters. For instance, in *Esox lucius* Stendell (1913) finds a pars intermedia, *Übergangsteil*, and pars anterior. Charipper (1937) studying the same species, calls Stendell's *Übergangsteil*, pars tuberalis. Scruggs (1939) finds no pars anterior in *Esox niger*, and calls Stendell's pars anterior, *Übergangsteil*. Matthews (1937) does not find an *Übergangsteil* in *Fundulus heteroclitus*, but Scruggs (1939) characterizes this structure as well developed in the same species. The apparently sudden appearance of the *Übergangsteil* in teleosts indicates the need of study of the holostean pituitary. Such study may prove of in-

terest in determining the status of the *Übergangstil*, even in the absence of physiological experiments, which still present serious practical difficulties.

Excepting the lack of the pars intermedia in birds, the pituitary in classes above the fishes is a fairly uniform structure consisting of the familiar three lobes, two buccal and one nervous in origin. In addition the pars tuberalis is developed to variable degrees within each vertebrate class but does not usually form an important part of the total hypophyseal volume. In reptiles the pars anterior is characteristically elongated and thin and most often curves anteriorly. The reptilian pars intermedia, if we may judge from the published work, has a greater volume than any other part of the gland. In birds the pars intermedia does not remain in the adult, or it may be present in extremely reduced form. This condition has been found in each of a rather considerable number of species examined (Painter and Rahn, 1939) and appears, therefore, to be common to all birds. The lack of a pars intermedia is quite rare in mammals. This condition has been reported, however, in several whales, the porpoise, and in the manatee—all aquatic forms—and also in the armadillo and elephant (Wislocki, 1929; Wislocki and Geiling, 1936; Oldham *et al*, 1938; Oldham, 1938). One wonders whether the loss of the pars intermedia was of any evolutionary value in these diverse animal groups. That the loss of the pars intermedia occurs only in those two classes of vertebrates which have also lost functional chromatophores seems to be only an interesting coincidence.

The site of production of melanophore hormone

It is a fact that in those animals which have no pars intermedia the melanophore hormone is found in the pars anterior. Even more surprising is the finding of

Kleinholz and Rahn (1939) that this hormone is present in the distal one-third of the chicken pituitary in an amount twenty times that present in the one-third portion immediately adjacent to the infundibulum. The occurrence of chromatophoretropic hormone in the pars anterior is, however, not peculiar to those forms lacking a pars intermedia. In sharks and rays Lewis and Butcher (1936) showed that melanophore hormone may be extracted from either the pars anterior or pars intermedia, but not from the pars ventralis. Highly suggestive evidence has been presented by Lewis (1936) who found this hormone in the tissue culture media in which either pars anterior or intermedia had been kept.

Comparative histophysiology of the anterior pituitary

The elasmobranch pars anterior is made up of cords and tubules between which is a very rich system of blood vessels. Eosinophilic cells are always found in the peripheral parts of these cords and tubules, next to the blood vessels. The inner cells have most often been described as chromophobe, but sometimes as weakly basophilic. The eosinophils predominate in younger animals during the period of active growth, but during "gestation" in viviparous sharks, when gonadotropic hormones are presumably being secreted in excess, chromophobes increase in number and eosinophils are restricted to the extreme periphery of each tubule. Carere Comes (1936) construes these data to indicate growth hormone secretion by acidophils and gonadotropic secretion by chromophobes in elasmobranchs.

In teleosts the fine early study of Bock (1928) of the pituitary of the Stickleback represents the only histophysiological work in bony fishes. Bock found no typical basophils in the pars anterior—only acidophils and chromophobes. The

same was true of the *Übergangsteil*. Using degranulation as an index of secretory activity, the pars anterior was found to exhibit no cyclic change throughout the year. The *Übergangsteil*, however, was rapidly degranulated in June and July. Acidophil granules were then slowly restored and reached a maximum level again in November and December. Unfortunately, no significant conclusions can be drawn from these facts until they can be correlated with more definite physiological activities.

In Amphibia Zahl (1935) has made similar cytological observations of the frog pituitary during the seasonal sex cycle. In frogs there is a gradual increase in acidophilic granules during the winter months. In the spring a sudden degranulation of acidophils occurs, during the period of sexual activity. Gonadotropic activity of the glands, when tested by the implant method by Zahl, appears to be correlated with a greater degree of granulation of acidophils. This work, if it can be said to locate gonadotropic hormone (reference is made to the primary or follicular stimulating component of the gonadotropic complex), production in the acidophils, is in apparent disagreement with the more firmly established data in birds and mammals. Thyroidectomy in the salamander *Triturus* produces a more orthodox result, namely vacuolization of basophils (Grobstein, 1938).

The anterior lobe of reptiles, like that of amphibia contains acidophils, basophils, and chromophobes. According to Altland (1939), basophilic cells increase in number during the breeding period of the lizard and may therefore be involved in gonadotropic secretion. During the remainder of the season the anterior lobe is predominantly acidophilic. Thyroidectomy in the snake (Siler, 1936) leads to enlargement and vacuolization of

basophils. In time these enlarged basophils become chromophobic and finally pycnotic.

Schildmacher (1937) has made a study of seasonal cytological changes in the anterior lobe of the robin *Turdus merula*. Basophils and chromophobes appear to remain uniform throughout the year, but eosinophils are found in significant numbers only during the spring breeding period. Schooley and Riddle (1938) have reported a rather complete histophysiological study of the pigeon pituitary. By correlating cytological structure with periods of growth, gonadal activity, brooding, and bioassays of hormone activity during these periods, they concluded that the acidophils are responsible for this "growth" effect and for crop-sac stimulation. Basophils can be correlated with gonadotropic and thyrotropic activity.

In summarizing the data purporting to reveal the physiological rôles of the different tinctorial cell types of anterior lobes of the lower vertebrates, it must be admitted that nothing but suggestive information now exists, excepting the somewhat better work in birds. The unsettled nature of these questions should invite further study, since existing data seem to indicate that in different species, even within a single class, different tinctorial cell types may be responsible for the formation of the same hormone.

Known occurrence of pituitary hormones

Many hypophysectomies have now been made in the lower vertebrates, and still more pituitary-injection experiments have been conducted in exploration of the extent of hypophyseal action in the various animal groups. This information has been summarized in Table I. However, certain unusual results obtained in

TABLE 1
The known occurrence of pituitary hormones

	CHROMATO- PHOTOTROPIN	GONADOTROPIN	THYROTROPIN	ADRENOTROPIN	GROWTH	PROLACTIN	DIABETOGENIC
Crustacean eye-stalk	+ (2)	..	..	..	..	..	..
Insect corpus allatum	..	+ (92) (73)	..	..	..	..	..
Ascidian subneural gland	..	+ (44) - (13)	..	..	..	..	..
Cyclostome	+ (99)	..	..	..	..	..	..
Elasmobranch	+ (58) (1)	..	..	..	..	..	..
Telcost	+ (1)	+ (46) (21) (49) (9) LH (97)	+ (37)	..	..	+? (32)	..
Amphibian	+ (Many re- ports) (1)	+ (Many reports) (48) (98) (27)	+ (85) (5) (4)	+ (20) (74)	+? (34)	+? (32) (35)	+ (47) (84)
Reptile	+ (50) (1)	+ (46) (78)	+ (78) (43)	..	..	+? (32)	..
Bird	+ (32) (51)	+ (Many reports) FSH (54) (65) LH (96) (54)	+ (96) (86) (37)	+ (65)	..	+ (52) (80) - (65)	..
Mammal	+ (Many re- ports)	+ (Many reports) FSH (Many reports) LH (Many reports)	+ (Many re- ports)	+ (Many re- ports)	+ (Many re- ports)	+ (Many re- ports)	+ (Many re- ports)

lower vertebrates deserve more than passing mention.

Comparative physiology of gonadotropic hormones

Since the establishment in mammals of separate luteinizing, follicle-stimulating, and other gonadotropic hormones, it has become of interest to determine the action of such fractions in gonads differing greatly from mammals in structure, and gonads lacking typically mammalian parts, like the corpus luteum. Conversely, the comparative physiologist wishes to learn whether the pituitary of lower vertebrates is capable of acting on structures which were evolved at a later time, in response to reproductive needs of a different sort. In *Triturus*, a salamander, FSH is considerably more effective in stimulating growth of ovaries in hypophysectomized animals than is LH; LH, on the other hand, is a considerably more effective reagent in inducing ovulation (Mayo, 1937). Amphibian pituitaries in mammals have never been given in high enough dosage to produce results of any note. Doses of 211 frog pituitaries (233 mg) produced only slight gonadal and uterine stimulation (in weight) in the mouse (Adams and Granger, 1938). Doses of 8 to 20 mg of African clawed-toad pituitary produced slightly more pronounced effects in immature mice (Zwarenstein, 1939). Such treatment gave *blutpunkts* and slight ovarian weight stimulation, opening of the vagina, and a two- to four-fold increase in weight of the uterus. The meager information provided by these experiments seems to indicate that amphibian pituitary contains a gonadotropic substance capable of acting in mammals, but its more exact nature cannot be determined without larger dosages of amphibian pituitary. It would seem from Mayo's work that the am-

phibian ovary, aside from the fact that it lacks a corpus luteum, responds quite similarly to the mammalian gonad to FSH and LH. However, the action of FSH in amphibia, although involved in the same *phase* of ovarian function, is actually producing a different end result. FSH in mammals stimulates follicular growth. FSH in amphibia, according to Mayo's work, stimulates *growth and maturation of the ovum*, which in mammals is a process which apparently proceeds independently of pituitary action. The work of Mayo on this important question deserves careful and extensive checking with more studies on hypophysectomized amphibia. In view of the finding that mammalian ovulation occurs after LH administration to females with ripe follicles the data of Mayo are quite regular. However, when one considers that ovulation is the only response of which a mature amphibian gonad is capable, and that human pregnancy and menopause urine, pregnant mare's serum, and pituitary preparations from many mammals have been successfully used to elicit this response, it seems that ovulation may not be so specific a reaction in amphibia after all. Even more surprising in this regard have been the recent publications of Shapiro (1939) and Zwarenstein (1937), who showed that ovulation in hypophysectomized *Xenopus*, the clawed-toad, can be induced by progesterone and a number of natural and synthetic androgens, but not by estrogens. They could even produce release of ova by adding these hormones to *in vitro* preparations of excised *Xenopus* ovary.

Mammalian pituitary FSH, LH, and gonadotropic antagonist preparations, and pregnant mare serum extract increase ovarian vascularity and increase ovarian weight by yolk deposition in the Horned toad (Mellish and Meyer, 1937). Rep-

tilian pituitary, on the other hand, has never been tried in the mammal. The ability of the various different mammalian gonadotropic fractions to stimulate growth of the ova would seem to indicate that this response may be as non-specific as ovulation appears to be in *Xenopus*. However, this possibility must be tested in hypophysectomized animals. L. T. Evans (1935) has found that urinary prolactin and sheep pituitary extract also stimulate ovarian growth in *Anolis*, but only the hypophyseal preparation will induce ovulation. Rahn (1939) has recently published good descriptions of the corpora lutea of various reptiles. It is unfortunately true that none of the recent workers using relatively purified gonadotropic fractions in reptiles has made observations on the physiology of the reptilian corpus. Cunningham and Smart (1934), using rather impure preparations of beef pituitary, stimulated ovulation in two viviparous lizards (*Anguis*, and *Zootoca*) and in one oviparous lizard, *Lacerta*. Corpora lutea were then found to develop in the two viviparous species. This work makes it especially desirable that the gonadotropic properties of reptile pituitaries be thoroughly investigated, since such work may shed some light on the problem of evolution of separate gonadotropic fractions. Several authors (Table I) have recently succeeded in finding LH in bird pituitaries, and since, according to some of these workers, the bird has no corpora lutea, LH appears phylogenetically before the corpus luteum itself. This statement may be questioned from two standpoints; (1) Mingazzini (1893), Cunningham and Smart (1934) and others have demonstrated the existence of a corpus in an ancestral group—the reptiles; (2) the birds themselves are at the end of an evolutionary line, so that the appearance of LH in this group does not antici-

pate any events in any other group of vertebrates. Since the reptiles were also the ancestral group for the Mammalia, corpora lutea in these two classes are probably homologous, and to find the origin of hypophyseal control over these new structures it seems now that we must investigate not only the reptilian pituitary but also that of more primitive forms. Recently Witschi (1939), has reported, in abstract, the occurrence of LH in the pituitary of the salmon, using a test based on a reaction of the regenerating feather of the Weaver-finch. If the validity of this finding can be confirmed by stimulation of luteinization in the usual assay procedures it would indeed be established that LH has arisen long before the organized corpus luteum. The possible function of a luteinizing hormone in the lower vertebrates presents many interesting possibilities. The apparent diversity of the action of LH on the amphibian ovary (Mayo, 1937) and on the feather of the Weaver-finch indicates that this problem probably has no simple solution.

FSH and LH in birds produce, respectively, germinal and interstitial cell stimulation, as they do in mammals. The very adequate researches of Witschi *et al.* (1937) and Meyer, Mellish, and Kupperman (1939) have demonstrated that turkey and chicken pituitaries both contain FSH and LH. It is more or less surprising to find that the bird gonad is especially non-responsive to prolactin, when the gonads of certain fish, amphibia, and reptiles can be stimulated by this substance.

Thyrotropic, adrenotropic and lactogenic hormones

As far as they have been studied, the thyrotropic and adrenotropic hormones, as well as their target organs themselves, have been quite uniform throughout the vertebrates and do not seem to offer any

important problem to the comparative physiologist. However, it might be of interest to investigate the action of thyrotropin and adrenotropin in the ammocoetes of lampreys, since the target organs in these animals present certain peculiarities.

Prolactin occupies a peculiar place in comparative endocrinology at the present time since Leblond and Noble (1937) have reported it in the pituitaries of every vertebrate class from the fishes on, and its target organ, the mammary gland, is not evolved until the mammals. Leblond and Noble, using Lyons' method of assay, obtained some results with fish, amphibian, and reptilian pituitaries which they themselves characterized as "prolactin-like" because they were not entirely typical. As many as fifty to one hundred fish pituitaries (*Ameiurus*) implanted subcutaneously at one site were required to give a "positive" test. Chicken pituitaries in their hands gave a rather strong prolactin reaction to a considerably smaller amount of pituitary tissue, but Meyer, Mellish, and Kupperman (1939) using the same test and the same pituitary source obtained negative results. Nevertheless, the action of this hormone in lower vertebrates should be examined very carefully, especially now that it is available in comparatively purified form. Noble, Kumpf, and Billings, (1938) found that prolactin induced brooding behavior in the Jewel-fish (*Hemichromis bimaculatus*), although progesterone was even more effective in this respect. These investigators did not look for any other effect of prolactin in the fish. Chadwick (1940) has recently identified prolactin as the hormonal stimulant for "water-drive" in the land stage *Triturus viridescens*. Any explanation of the presence of prolactin in the pituitaries of the lowest vertebrates is no more than a guess, but it might be profitable in this case to venture a reason-

able guess to indicate the manner in which this problem might be attacked. It could be that prolactin has a still unrecognized function, perhaps serving as (1) a parental or "care of the young" hormone, in lower vertebrates, or (2) since it is of such general occurrence, and since Riddle seems to have shown its close relation to the growth effect, it might serve as a special growth hormone affecting definite organs, like abdominal viscera. The recent chemical data of Evans (1939) and his co-workers appear to rule out any possibility of identity of prolactin with the classical growth hormone.

Instances of unusual actions of pituitary hormone

We are accustomed to regard the secondary and accessory sex characters of vertebrates as being subject to the control of the gonadal hormones. Yet there are at least three instances in lower vertebrates in which such characters have been claimed under the direct influence of hypophyseal hormones. Guyenot, Moskowska, and Ponse (1932) found that the nuptial thumb pads of male toads, *Bombinator pachypus*, could be stimulated in castrate animals by pituitary implants. It is known that in other amphibia this structure can be stimulated by the pituitary only in the presence of an intact testis. De Allende (1938) using another toad, *Bufo arenarum*, has published the surprising statement that pituitary implants will stimulate secretory activity in the oviduct of castrates, but *large doses of estrone will not!* Finally, Witschi (1937) has demonstrated that pituitary preparations can induce cock-feathering in castrate African finches (*Pyromelana*, *Steganura*, or *Quelea*). His data seem to indicate that LH is directly responsible for this effect, and in fact he suggests the use of such birds for the bioassay of LH.

Environmental influences on the pituitary

We have been considering at some length the control by the pituitary over certain secondary organs and processes in the vertebrates. We must now consider the factors which have been found to stimulate activity of the pituitary. This problem is especially important in the understanding of those conditions in which cyclic changes in pituitary activity have been found to occur. In most vertebrates this cycle is annual. In mammals shorter oestrous cycles may be superimposed on the annual cycle. In some cases, as in the rat and in man, the annual cycle may be lost. At least a part of the factors involved in these regular fluctuations of endocrinal activity are now understood—primarily from work with birds by Marshall (1936), Bissonette (1936, 1937) and Rowan (1938). The number of comprehensive reviews of the subject of environmental control over pituitary activity, by these and other authors makes it unnecessary to include here more than a brief summary. In many birds successively additive or subtractive amounts of daylight or of wakefulness have been found to influence the activity of the pituitary and its secondary organs. On the other hand, this procedure is not effective in all birds tested, such as tropical birds, living in an environment in which the length of the day is fairly constant. This suggests that the method of hypophyseal control evolved may vary, even within smaller taxonomic groups. Certain fish (Stickleback) can be made to breed out of season by raises in temperature and will not respond in the light-ration experiment (Craig-Bennet, 1930), although this claim has been criticized (Tinbergen in Rowan, 1938). Other fish (trout) do respond in light-ration experiments (Hoover and Hubbard, 1937). It

has been suggested that temperature changes are not regular enough to be suitable in guiding the breeding behavior of freshwater fish, but the high specific heat of water and the tremendous volume of the sea make temperature changes in the ocean regular enough to be useful to marine animals. These factors, light duration, wakefulness, and temperature, are manifestly of the greatest importance in those instances in which they are operative, but no doubt there are other avenues of nervous stimulation of the pituitary, e. g., copulation in the cat and rabbit, and the visual stimulation provided by the presence of eggs in the sparrow's nest. These facts do not as yet offer any means for a better understanding of the mammalian oestrous cycle, but do represent an advance in our knowledge of pituitary physiology. Through such factors as have been discussed, evolution has involved the pituitary in such spectacular phenomena as migration of entire populations of birds and fishes.

Species differences in hypophyseal hormones

Much of the exploratory work in lower vertebrates has been discouraging because the results of hormone injection have not been clear-cut, or because of the relatively massive dosages required to yield a minimum response. Because of this relative inefficiency of mammalian pituitary preparations in many lower vertebrates some workers have suggested that a pituitary hormone species-specificity might exist. Other workers, having found a lower vertebrate species which will respond to large doses of mammalian pituitary, make the opposite claim. This problem is of primary importance in the interpretation of bioassay values when the pituitary donor and the test animal are of widely divergent taxonomic types. For example, under favorable conditions the salamander

Triturus pyrrhogaster can be made to ovulate with a minimum dose of 200 rat units of sheep pituitary gonadotropic extract. Two or three frog pituitaries (*Rana pipiens*) will produce the same effect. According to the usual practice of equating rat, rabbit, bird, and other units, one frog pituitary would be equivalent to about 100 rat units of mammalian gonadotropic substance. But we know that this is not true from the work of Adams and Granger (1938) who found that 211 *Rana pipiens* pituitaries are needed to elicit even slight ovarian stimulation in an immature mouse. It may be well to regard the species factor seriously even when dealing with different mammalian hormones in mammalian test animals. In evaluation of this loss in efficiency of a pituitary hormone when administered to animals having more and more remote relation to the donor species Creaser and Gorbman (1936, 1939) and Benazzi (1939) have referred to a "relative species specificity." It is not difficult to find a probable physical basis for this phenomenon when it is remembered that the pituitary hormones have been shown to be protein in nature. It is well known that corresponding proteins vary sufficiently, even between closely related species, to make possible detection of their variation by immunological methods. Of the pituitary hormones, the lactogenic has recently become isolated as a pure protein. Using such preparations of lactogenic hormone from sheep and beef pituitaries, Li, Lyons, and Evans (1940, 1941) have been able to demonstrate an actual difference in solubility and in content of the amino acid tyrosine, even between these relatively closely related ungulates. Conceivably, the opportunities for protein hormone variation between

widely divergent taxonomic groups have been many, and the change in the hormone can finally become great enough to become detectable physiologically in hormone exchanges between species.

SUMMARY

The most primitive living vertebrates already possess a fully differentiated pituitary body. The evolutionary antecedents of the pituitary body are unknown, and it does not seem probable that they shall ever be found.

Within the vertebrate group the structural relationships of the parts of the pituitary are fairly constant. The most remarkable variations are the presence of a "ventral" lobe in elasmobranchs, the presence of an *Übergangsteil* in teleosts, and the absence of the pars intermedia in birds and some mammals.

Exploration and comparison of the hormone content of pituitaries of lower vertebrates with mammals is still far from complete, but several interesting conditions have been shown to exist. The presence of the luteinising hormone has been claimed for the hypophyses of fish and birds, neither of which has corpora lutea. The lactogenic hormone has been reported in all vertebrate classes, but its "target organ" is found only in one.

Environmental factors influencing cyclical activity of the pituitary may be of a different nature even within rather closely related vertebrate groupings.

The reduced efficiency of administered pituitary hormones from very divergent species may be explained by the concept of a "relative species-specificity."

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LIST OF LITERATURE

1. ABRAMOWITZ, A. A. 1937. The chromatophoretic hormone of the Crustacea: standardization, properties and physiology of the eye-stalk glands. *Biol. Bull.*, 72: 344-365.
2. —. 1939. Color changes in animals. *Tabulae Biol.*, 17: 265-337.
3. ADAMS, A. E., and GRANGER, BARBARA. 1938. Stimulation of the reproductive tract of the infantile female mouse by anuran anterior pituitary substance. *Proc. Soc. Exp. Biol. and Med.*, 38: 585.
4. —, —, and RHOADES, R. 1938. Stimulation of the thyroid gland of the guinea pig by anuran anterior pituitary. *Anat. Rec.*, 72: 491-498.
5. ALLEN, B. M. 1929. The influence of the thyroid gland and the hypophysis upon growth and development of amphibian larvae. *QUART. REV. BIOL.*, 4: 325-352.
6. DE ALLENDE, INES L. C. 1938. Influencia directa de la hipófisis sobre el oviducto de los batracios. *Rev. Soc. Arg. Biol.*, 14: 505-508.
7. ALTLAND, P. D. 1939. Cytology of the hypophysis of the fence lizard. *Anat. Rec.*, 74: 109-123.
8. ATWELL, W. J. 1935. Effects of thyrotropic and adrenotropic principles on hypophysectomized amphibia. *Anat. Rec.*, 62: 361-379.
9. DE AZEVEDO, P., and CANALE, L. 1938. The pituitary and its action on the gonads of neotropical fishes. *Arch. Inst. Biol., São Paulo*, 9: 165-186.
10. BACQ, Z. M., and FLORKIN, M. 1935. Mise en évidence, dans le complexe "ganglion nerveux-glande neurale" d'un Ascidie (*Ciona intestinalis*) de principes pharmacologiquement analogues à ceux du lobe postérieur de l'hypophyse des Vertébrés. *Arch. Int. Physiol.*, 40: 422-428.
11. BATESON, W. 1886. The ancestry of the Chordata. *Quart. Jour. Micro. Sci.*, 26: 537-571.
12. BENAZZI, M. 1939. Esperienze intorno alla ovulazione provocata negli Anfibi. *Monist. Zool. Ital.*, 50: 101-107.
13. —. 1939. Sul significato funzionale della ghiandola neurale (presunta ipofisi) delle Ascidie. *Boll. di Zool.*, 10: 99-103.
14. VAN BENEDEK, ÉD., and JULIN, C. La segmentation chez les Ascidien et ses rapports avec l'organisation de la larve. *Arch. de Biol.*, 5: 111-126.
15. BICKFORD, E. 1895. The hypophysis of the *Calamocathys calabaricus* (Smith). *Anat. Anzeig.*, 10: 465-470.
16. BISONNETTE, T. H. 1936. Sexual photoperiodicity. *QUART. REV. BIOL.*, 11: 371-386.
17. —. 1937. Photoperiodicity in birds. *Wilson Bull.*, 49: 241-270.
18. BOCK, F. 1928. Die Hypophyse des Stichlings (*Gasterosteus aculeatus* L.) unter besonderer Berichtigung der Jahreszyklischen Veränderungen. *Zeitschr. wiss. Zool.*, 131: 645-710.
19. BRAMBELL, F. W. ROGERS, and COLE, H. A. 1939. The preoral ciliary organ of the Enteropneusta: its occurrence, structure, and possible phylogenetic significance. *Proc. Zool. Soc. London*, B, 109: 181-193.
20. BROWN, A. L. 1920. The results of the extirpation of the thyroid and of the pituitary anlagen on the interrenal tissue in *R. pipiens*. *Anat. Rec.*, 17: 326.
21. CARDOSO, D. M. 1934. Relação genito-hipofisaria e reprodução nos peixes. *Arch. Inst. Biol., São Paulo*, 5: 133-136.
22. CHARIPPER, H. A. 1937. The morphology of the hypophysis in lower vertebrates, particularly fish and amphibia, with some notes on the cytology of the pituitary of *Incarassius auratus* (the Goldfish) and *Necturus maculosus* (the Mudpuppy). In *Cold Spring Harbor Symposia on Quant. Biol.*, 5: 151-164.
23. COMES, O. CARRE. 1936. Sulla funzione delle cellule eosinofile e cromofobe nel lobo anteriore dell' ipofisi. *Boll. Soc. Ital. Biol. Sper.*, 11: 216-218.
24. CRAIG-BENNETT, A. 1930. The reproductive cycle of the three-spined stickleback. *Phil. Trans.*, B, 219: 197-279.
25. CHADWICK, C. S. 1940. Identity of prolactin with water drive factor in *Triturus viridescens*. *Proc. Soc. Exp. Biol. and Med.*, 45: 335-337.
26. CREASER, C. W., and GORSMAN, A. 1936. Specificity of the pituitary gonadotropic factor as demonstrated in amphibia. *Copeia*, no. 2: 91-94.
27. —, —. 1939. Species specificity of the gonadotropic factors in vertebrates. *QUART. REV. BIOL.*, 14: 311-331.
28. CUNNINGHAM, J. T., and SMART, W. A. M. 1934. The structure and origin of corpora lutea in some of the lower Vertebrata. *Proc. Roy. Soc., London*, 116B: 258-281.
29. DE BEER, G. R. 1923. Some observations on the hypophysis of *Petromyzon* and of *Amia*. *Quart. Jour. Micro. Sci.*, 67: 257-292.

30. —. 1926. The Comparative Anatomy, Histology and Development of the Pituitary Body. Oliver and Boyd, London.
31. DELAGE, Y., and HÉROUARD, E. 1898. Les Procordés. *Traité de Zoologie Concrète*, Tome 8.
32. DE LAUDER, H. M., TARR, L., and GEILING, E. M. K. 1934. Distribution in the chicken's hypophysis of the so-called posterior lobe principles. *Jour. Pharm. Exp. Therap.*, 51: 142-143.
33. EVANS, L. T. 1935. The effect of antuitrin-S and sheep pituitary extract on the female lizard, *Anolis carolinensis*. *Biol. Bull.*, 68: 355-359.
34. FOGLIA, V. G. 1940. Acción de la hipofisis del sapo *Bufo arenarum* Hensel sobre las suprarrenales, timo y bazo de los mamíferos. *Rev. Soc. Arg. Biol.*, 16: 511-522.
35. —. 1940. Acción de la hipofisis del sapo *Bufo arenarum* Hensel sobre el buche de la paloma. *Rev. Soc. Arg. Biol.*, 16: 559-562.
36. GERRARD, P., and CORDIER, R. 1936. Sur la région infundibulohypophysaire de *Polypterus weeksii*. *Compt. Rend. Ass. Anat.*, 31 Sess., Milan: 160-169.
37. GORBMAN, A. 1940. Suitability of the common goldfish for assay of thyrotropic hormone. *Proc. Soc. Exp. Biol. and Med.*, 45: 772-773.
38. GRAY, S. W., and FORD, W. 1940. The effect of the crustacean eye-stalk hormone upon water metabolism and melanophore expansion in the frog. *Endocrinology*, 26: 160-162.
39. GRIFFITHS, M. 1938. Studies on the pituitary body. II. Observations on the pituitary in dipnoi and speculations concerning the evolution of the pituitary. *Proc. Linnean Soc., N. S. Wales*, 63: 88-94.
40. GROBSTEIN, C. 1938. Appearance of vacuolated cells in hypophysis of *Triturus torosus* following bilateral thyroidectomy. *Proc. Soc. Exp. Biol. and Med.*, 38: 801-803.
41. GUYENOT, E., MOSKOWSKA, A., and PONEB, K. 1932. Action directe de l'hypophyse sur les excroissances nuptiales de *Bombinator pachypus*. *Compt. Rend. Acad. Sci.*, 194: 206-208.
42. HARMER, S. F. 1897. On the notochord of *Cephalodiscus*. *Zool. Anzeig.*, 20: 342-346.
43. HELLBAUM, H. W. 1936. The cytology of snake thyroids following hypophysectomy, activation, and ultra-centrifuging. *Anat. Rec.*, 67: 53-63.
44. HOOB, B. M. 1937. Subneural gland of an Ascidian, (*Polycarpa tecta*), an ovarian stimulating action in immature mice. *Proc. Soc. Exp. Biol. and Med.*, 35: 616.
45. HOOVER, E. E., and HUBBARD, H. E. 1937. Modification of the sexual cycle in trout by control of light. *Copeia*: 206-210.
46. HOUMAY, B. A. 1930. Acción sexual de la hipofisis en los peces y reptiles. *Rev. Soc. Arg. Biol.*, 6: 686-688.
47. —, and BIAMOTTI, A. 1936. Rôle de l'hypophyse et de la surrénale dans le diabète pancréatique du crapaud. *Compt. rend. Soc. de Biol.*, 123: 497-500.
48. —, GIUSTI, L., and LASCANO-GONZALEZ, J. M. 1929. Implantation d'hypophyse et stimulation des glandes et des fonctions sexuelles du crapaud. *Compt. rend. Soc. de Biol.*, 102: 864-866.
49. VON IHERING, R., and DE AZEVEDO, P. 1936. A desova e a hypophysação das peixes; Evolução de dois nematognathas. *Arch. Inst. Biol., São Paulo*, 7: 107-117.
50. KLEINHOLZ, L. H. 1938. Reptilian color changes. II. Pituitary and adrenal glands in regulation of the melanophores of *Anolis carolinensis*. *Jour. Exp. Biol.*, 15: 474-491.
51. —, and RAHN, H. 1939. The distribution of intermedin in the pars anterior of the chicken pituitary. *Proc. Nat. Acad. Sci.* 25: 145-147.
52. LEBLOND, C. P., and NOBLE, G. K. 1937. Prolactin-like reaction produced by hypophysis of various vertebrates. *Proc. Soc. Exp. Biol. and Med.*, 36: 517-518.
53. LEGROS, R. 1909. Sur le développement des fentes branchiales et de canalicules de Weisss-Boveri chez l'amphioxus. *Anat. Anzeig.*, 34: 126-151.
54. LEONARD, S. L. 1937. Luteinizing hormone in bird hypophyses. *Proc. Soc. Exp. Biol. and Med.*, 37: 566-568.
55. LEWIS, M. R. 1936. Further studies on the hypophysis cerebri of certain selachians by means of tissue cultures. *Bull. Mount Desert Island Biol. Lab.*, 1936: 22.
56. LI, C. H., LYONS, W. R., and EVANS, H. M. 1940. Studies on pituitary lactogenic hormone. IV. Tyrosine and tryptophane content. *Jour. Biol. Chem.*, 136: 709-712.
57. —, —, —. 1941. Studies on pituitary lactogenic hormone. VI. Molecular weight of the pure hormone. *Jour. Biol. Chem.* (in press).
58. LEWIS, M. R., and BUTCHER, E. O. 1936. The melanophore hormone of the hypophysis cerebri of certain selachians. *Bull. Mount Desert Island Biol. Lab.*, 1936: 20-21.
59. MARSHALL, F. H. A. 1936. Sexual photoperiodicity and the causes which determine it.

- The Croonian Lecture. *Phil. Trans. Roy. Soc. London*, 226: 423-456.
60. MASTERMAN, A. T. 1899. On the "Notochord" of *Cephalodiscus*. *Zool. Anzeig.*, 22: 359-363.
 61. MATTHEWS, S. A. 1937. Development of the pituitary gland in *Fundulus*. *Biol. Bull.*, 73: 93-98.
 62. MAYO, VIRGINIA. 1937. Some effects of mammalian follicle-stimulating and luteinizing hormones in adult female urodeles. *Biol. Bull.*, 73: 373.
 63. MEAMBER, D. L., FRAENKEL-CONRAT, H. L., SIMPSON, M. E., and EVANS, H. M. 1939. The preparation of pituitary growth hormone free from lactogenic and thyrotropic hormones. *Science*, 1939, II: 19-20.
 64. MELLISH, C. H., and MEYER, R. K. 1937. The effects of various gonadotropic substances and thyroxin on the ovaries of horned lizards (*Phrynosoma cornutum*). *Anat. Rec.*, 69: 179-189.
 65. MEYER, R. K., MELLISH, C. H. and KUPPERMAN, S. 1939. The gonadotropic and adrenotropic hormones of the chicken hypophysis. *Jour. Pharm. Exp. Therap.*, 65: 104-114.
 66. MINGAZZINI, P. 1893. Corpi lutei veri e falsi dei Rettili. *Roma Lab. Anat. Norm. Rich.*, 3: 105-126.
 67. NOBLE, G. K., KUMPF, K. F., and BILLINGS, V. N. 1938. Induction of brooding behavior in Jewel Fish. *Endocrinology*, 23: 353-359.
 68. NORRIS, H. W. 1936. The general morphology of the elasmobranch hypophysis. *Anat. Rec.*, 64 supp. No. 1: 35.
 69. OLDHAM, F. K. 1938. The anatomy and pharmacology of the hypophysis of the armadillo. *Anat. Rec.*, 72: 265-290.
 70. —, McLEERY, D. P., and GEILING, E. M. K. 1938. A note on the histology and pharmacology of the hypophysis of the Manatee (*Trichechus inunguis*). *Anat. Rec.*, 71: 27-32.
 71. PAINTER, B. T., and RAHN, H. 1939. A comparative histology of the bird pituitary. *Anat. Rec.*, 78 supp.: 89.
 72. PATTEN, W. 1912. The Evolution of the Vertebrates and Their Kin. P. Blakiston's Son and Co., Philadelphia.
 73. PFEIFFER, I. W. 1939. Experimental study of the function of the corpora allata in the grasshopper, *Melanoplus differentialis*. *Jour. Exp. Zool.*, 82: 437-461.
 74. PORTO, J. 1940. Relaciones entre la hipofisis y la adrenal en el sapo. *Rev. Soc. Arg. Biol.*, 16: 489-494.
 75. RAHN, HERMANN. 1939. The corpus luteum of reptiles. *Anat. Rec.*, 72 supp.: 55.
 76. ROMER, A. S. 1933. Vertebrate Paleontology. University of Chicago Press, Chicago.
 77. ROWAN, WM. 1938. Light and seasonal reproduction in animals. *Biol. Rev.*, 13: 374-402.
 78. SCHARFER, W. H. 1933. Hypophysectomy and thyroidectomy of snakes. *Proc. Soc. Exp. Biol. and Med.*, 30: 1363-1365.
 79. SCHILDMACHER, H. 1937. Histologische Untersuchungen an Vogelhypophysen. I. Die Zelltypen der Amsel, *Turdus merula* L. *Jour. Ornith.*, 85: 587-592.
 80. SCHOOLEY, J. P., and RIDDLE, O. 1938. The morphological basis of pituitary function in pigeons. *Am. Jour. Anat.*, 62: 313-349.
 81. SCRUGGS, W. M. 1939. The epithelial components of the teleost pituitary gland as identified by a standardized method of selective staining. *Jour. Morph.*, 65: 187-213.
 82. SHAPIRO, H. A. 1939. Ovulation in *Xenopus laevis* induced by certain steroids. *S. Afr. Jour. Med. Sci.*, 4, supp.: 21-31.
 83. SILER, K. A. 1936. The cytological changes in the hypophysis cerebri of the Garter Snake (*Thamnophis radix*) following thyroidectomy. *Jour. Morph.*, 59: 603-623.
 84. SLOMB, D. 1936. The diabetogenic hormone of the pituitary gland. *Jour. Exp. Biol.*, 13: 1-6.
 85. SMITH, P. E. 1920. The pigmentary, growth, and endocrine disturbances induced in the anuran tadpole by the early ablation of the pars buccalis of the hypophysis. *Amer. Anat. Mem.*, II: 1-112.
 86. STEIN, K. F. 1934. Effects of avian pituitary glands in salamanders. *Proc. Soc. Exp. Biol. and Med.*, 32: 157-161.
 87. STENDBELL, W. 1913. Zur vergleichenden Anatomie und Histologie der Hypophysis cerebri. *Arch. mikrosk. Anat.*, 82: 289-332.
 88. STENHÖ, ERIK A. 1927. The Downtonian and Devonian vertebrates of Spitzbergen. Part I. Family Cephalaspidae. *Oslo*.
 89. TILNEY, F. J. 1911. Contribution to the study of the hypophysis cerebri with especial reference to its comparative histology. *Memoirs Wistar Inst. Anat. and Biol.*, No. 2.
 90. —. 1937. The hypophysis cerebri of *Petromyzon marinus dorsatus*. *Bull. Neurol. Inst.*, New York, 6: 70-117.
 91. TRETIKOFF, D. 1929. Ursprung der Chordaten. *Zeitschr. Wiss. Zool.*, 134: 558-640.

92. WIGGLESWORTH, V. 1934. *Insect Physiology*. Methuen and Co., London.
93. WILLEY, ARTHUR. 1899. *Zoological Results. Part III*. Cambridge University Press, Cambridge.
94. WISLOCKI, G. B. 1929. The hypophysis of the porpoise (*Tursiops truncatus*). *Arch. Surg.*, 18: 1403-1412.
95. —, and GELING, E. M. K. 1936. The anatomy of the hypophysis of the whale. *Anat. Rec.*, 66: 17-36.
96. WITCHT, E. 1937. Comparative physiology of the vertebrate hypophysis (anterior and intermediate lobes). In *Cold Spring Harbor Symposium on Quant. Biol.*, 5: 180-190.
97. —. 1939. Quantitative determination of the follicle stimulating and the luteinizing hormone of the hypophysis. *Anat. Rec.*, 75, supp.: 58.
98. WOLF, O. M. 1929. Effect of daily transplants of anterior lobe of pituitary on reproduction of frog. *Proc. Soc. Exp. Biol. and Med.*, 26: 692-693.
99. YOUNG, J. Z. 1935. The photoreceptors of lampreys. II. The functions of the pineal complex. *Jour. Exp. Biol.*, 12: 254-270.
100. ZAHL, P. A. 1935. Cytological changes in frog pituitary considered in reference to sexual periodicity. *Proc. Soc. Exp. Biol. and Med.*, 33: 56-58.
101. ZWARENSTEIN, H. 1937. Experimental induction of ovulation with progesterone. *Nature*, 139: 112-113.
102. —. 1939. Induction of precocious sexual maturity in immature female mice with amphibian anterior pituitary. *S. Afr. Jour. Med. Sci.*, 4, supp.: 18-20.





OBSERVATIONS AND EXPERIMENTS ON MATING BEHAVIOR IN FEMALE MAMMALS (*Concluded*)

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FACTORS INVOLVED IN THE INDUCTION OF MATING BEHAVIOR AND IN THE REGULATION OF ITS CHARACTER

THE induction of mating behavior in female mammals is the result of very complex processes. The interaction of endocrine, neural, genetic, ontogenetic, nutritional, environmental, psychological, pathological and age factors is known to be involved and doubtless others are important. Because of this complex background, the part played by each factor is difficult to determine. In the normal animal a given combination of ovarian hormones may induce heat, but their production depends on an interplay of extrinsic and intrinsic factors and the character of the response they elicit may be determined by the reactivity of the soma they stimulate and the elements of the external situation in which the animal is living. Nevertheless, in any discussion of the subject, some starting point must be chosen. In what follows the ovarian hormones have been selected, not because they are necessarily the exclusive limiting factor, but because they are the means to the induction of heat by experimental procedures and the means by which the rôle of the other factors can be elucidated.

Ovarian hormones

The factors immediately responsible for the display of the estrous responses have

long been known to be ovarian in origin because complete ovariectomy is invariably followed by a cessation of cyclic reproductive activity. The willingness of rabbits to copulate within 48 hours after ovariectomy (Hammond and Marshall, 25; Reynolds, 31) and the display of heat recorded for the rat on the first day after the operation (Hemmingsen, 33) do not militate against this generalization. Post-operative heat, when it occurred, probably can be accounted for by the supposition that the animals were in heat at the time of the operation or that the operation was performed shortly before heat but after the effective stimulus had begun to operate. Nor does Robson's (38) report of a spayed *Macacus rhesus* monkey which permitted copulation discount the importance of the ovary. In mature monkeys, as in man, psychological factors may influence a situation which in lower mammals is under rigid hormonal control.

The identity of the hormones which induce normal heat responses in the rat and guinea pig became apparent only gradually. Those responsible for estrus in the other laboratory mammals and in wild species are not yet known with certainty. The first adequately controlled experiments were those of Allen (23), Allen and Doisy (23) and Allen, Francis, Robertson, Colgate, Johnston, Doisy, Kountz and Gibson (24) on spayed mice

and rats. Following the injection of follicular fluid extracts into 11 animals which were observed for evidences of mating, the indication of coitus in 7 (2 rats and 5 mice) was taken as evidence for the conclusion that estrous instincts are stimulated by the action of the follicular fluid hormone named "oestrin" by Parkes (29). Discounting the numerous experiments in which the observations were limited to the vaginal condition, what were regarded as confirmatory results were later obtained by Bourg (31), Hemmingsen (33), Kun (35) and Ball (36a). The irregularity with which mating responses were induced by injections of estrin was generally noted (Parkes, Fielding and Brambell, 27; Hemmingsen, 29, 33; Marrian and Parkes, 30; Wiesner and Mirskaia, 30), but was attributed to a postulated high threshold for mating (Marrian and Parkes, 30; Wiesner and Mirskaia, 30).

Although numerous investigators had postulated that the action of an additional factor might be involved (Asdell and Marshall, 27; Frei and Lutz, 29; Parkes, 29; Wiesner and Mirskaia, 30; Grant, 34; Witschi and Pfeiffer, 35; and Young, Dempsey and Myers, 35a), the suggestion was not considered seriously until Dempsey, Hertz and Young (36) showed that the induction of heat with any degree of regularity in the guinea pig depends on the synergistic action of estrogen and progesterone. Furthermore, when estrogen is followed by progesterone, large quantities of the former hormone are not necessary except in the few animals which are relatively insensitive to the conditioning action of estrogen (Boling, Young and Dempsey, 38). Recently estrogen and progesterone given in sequence to the rat have been found to be more effective than estrogen alone (Boling and Blandau, 39; Boling, Blandau, Rundlett,

and Young, 41). Ball (39), injecting the two hormones somewhat differently, did not have the same degree of success with rats of the strain she used.

When the results from the experiments by Dempsey, Hertz and Young were first announced, doubt was expressed that progesterone is produced prior to ovulation which is when heat begins, but the luteinization of cells of the theca interna and stratum granulosum as early as the first day of heat in the mare (Seaborn, 25), the cessation of uterine motility between the 5th and 8th hour after copulation in the rabbit (Reynolds and Friedman, 30; Reynolds and Allen, 32), the positive Bitterling ovipositor test for progesterone given by follicular fluid from the sow and cow (Duyvené de Wit, 38), and the decrease in water content of the rat's uterus prior to ovulation (Astwood, 39) attest to the probability of its presence in the unruptured follicle.

The suggestion was also made that a supplementary injection of estrogen might be as effective as progesterone, but thus far only negative results have followed this procedure in the guinea pig (unpublished data) and in the rat (Boling and Blandau, 39).

If the observations summarized above may be assumed to be conclusive, heat in the normal female guinea pig and rat is stimulated by the conditioning action of estrogen followed by the secondary action of progesterone produced in the maturing follicle. Following tests of 7 closely related compounds, Hertz, Meyer and Spielman (37) reported that in this respect the action of progesterone is specific. Since then, however, Soderwall (40) has found that pregnenolone given orally is effective, van Heuverswyn, Collins, Williams and Gardner (39) have reported that desoxycorticosterone acetate will also induce heat following a conditioning

injection of estrogen, and Torstveit and Mellish (41) state that adrenal cortical extracts act similarly. In their animals, the interval between the injection of the desoxycorticosterone acetate and the beginning of heat is longer than that worked out by Collins, Boling, Dempsey and Young (38).

The estrogen conditioning action is not limited to any one compound. Although no systematic investigation has been made, several substances which are known to induce vaginal cornification have also been found to be estrogenic in the sense that they induce the mating responses alone or in combination with progesterone when injected into spayed animals. In the work on the rat and guinea pig done by Blandau, Boling, Collins, Dempsey, Hertz and Young, estrone and estradiol benzoate were used. Success has also been reported following the injection of estriol and 9:10-dihydroxy-9:10-di-n-propyl-9:10-dihydro-1:2:5:6-dibenzanthracene into rats (Hemmingsen and Krarup, 37a), triphenyl ethylene into mice, hypophysectomized rabbits (Robson and Schönberg, 37) and a dog (Robson, 38), and stilbestrol di-ethyl into rats (Dodds, Lawson and Noble, 38) and guinea pigs (Leighty and Wick, 39; Leighty, Wick and Jeffries, 41).

In any theory of the hormonal factors involved in the induction of heat in the guinea pig and rat allowance must be made for the effective action of estrogens in many animals. There is no question but that large quantities of estrogen stimulate mating responses in a large percentage of individuals. Indeed Stone and Gibb (41) have recently induced estrus in all of fifteen rats by an initial injection of 1000 I.U. Theelin followed by 666 I.U. daily. Two questions, however, are critical: Do animals which fail to respond to the largest quantities of estro-

gen display estrous reactions when they are injected with the two hormones? When an estrogen induced heat is shown, is it strictly comparable with the heat displayed by normal animals and with the estrogen-progesterone induced heat in spayed animals? Guinea pigs and rats that were refractory to estrogen alone responded to supplementary injections of progesterone in the experiments by Dempsey, Hertz and Young (36), Boling and Blandau (39) and Boling, Blandau, Rundlett and Young (41). Ball (39) has not had the same success, but her procedure was different. The second question has received some attention for the guinea pig (Boling, Young and Dempsey, 38) and rat (Boling and Blandau, 39). In both species the estrogen- and the estrogen-progesterone-induced heat differ in at least two details. The estrogen-induced heat does not always rise at once to its greatest intensity and then taper off gradually to the non-estrous state, and it tends to be longer.

The results suggest that in the guinea pig and rat, by some mechanism which is completely obscure, the estrogens are very nearly able to stimulate normal heat responses, but for some reason they fall short, and that progesterone, likewise by means of a mechanism of which we have no knowledge, has a supplementary rôle on which the appearance of normal heat responses depend.

Indications are that both individual and species differences exist with respect to the extent estrogens are effective. Adult guinea pigs have been encountered in which heat did not occur prior to ovariectomy, but after ovariectomy it was induced when twice the usual conditioning quantity of estrogen was injected (Boling, Young and Dempsey, 38). Before their ovaries were removed these animals showed normal vaginal changes and probably would have

been capable of normal reproduction if properly timed artificial insemination had been made (Soderwall and Young, 40), but as far as the stimulation of mating activity is concerned, they are assumed to have been relatively insensitive to the conditioning action of estrogen. Individual differences in sensitivity to estrogens have also been found in rats (Hemmingsen, 33; Hemmingsen and Krarup, 37a; Boling and Blandau, 39; Boling, Blandau, Rundlett and Young, 41).

The existence of species differences is suggested by a comparison of data obtained from the rat and guinea pig. The percentage of rats which responded to given quantities of estrogen was higher than the percentage of guinea pigs which responded to comparable quantities (Boling and Blandau, 39; Dempsey, Hertz and Young, 36). Furthermore, untreated rats in which the luteinizing action was insufficient to cause ovulation have been found in heat (Boling, Blandau, Soderwall and Young, 41), whereas in the untreated guinea pig heat without ovulation has not been encountered (Young, Dempsey, Myers and Hagquist, 38).

Since the species which have been investigated show differences in their sensitivity to estrogens, it is reasonable to expect that the range of variation will be found to be great when additional species are studied. In fact, many may be encountered in which the mating responses are normally induced by estrogens alone. The possibility is suggested by three groups of observations.

The first is that estrogens alone have been sufficient to induce heat in spayed rabbits (Lacassagne and Gricouloff, 25; Büttner and Wienert, 35), spayed and anestrus sheep (Cole and Miller, 35; McKenzie and Terrill, 37), spayed mares (Neves e Castro, 38), spayed cats (Bard, 36, 39; Maes, 39, 40b), spayed and anes-

trous dogs (Kunde, D'Amour, Carlson and Gustavson, 30; Robson and Henderson, 36; Leathem, 38; Robson, 38; Sammartino and Arenas, 39), and spayed monkeys (Ball, 36b; Hartman, 38). To be sure, the quantity of injected estrogen was usually large and the results frequently irregular. Consequently, the rôle of progesterone cannot be excluded until the action of smaller quantities of estrogen followed by progesterone has been tested.

The possibility that estrogen alone is sufficient to induce heat in some species is suggested, secondly, by the fact that, following the injection of gonadotrophic hormones extracted from human menopausal or pregnancy urine, mating responses have been displayed by dogs before there is any visible evidence of luteinization (Swingle, Parkins, Taylor, Hays and Morrell, 37; Leathem, 38; Leathem and Morrell, 39). Here again, though, judgment must be withheld until it is known that follicular fluid in follicles at the stage of development when estrus begins contains only estrogen. Morphological evidence for the presence of progesterone in such follicles in the rabbit, guinea pig, rat, cow, and sow is absent; nevertheless physiological evidence suggesting that it is present has been cited.

A third group of observations is perhaps most convincing that in some species estrogen is sufficient for the induction of mating responses. In the cat, rabbit and ferret, and occasionally in the mare, heat is displayed prior to the time of the pre-ovulatory swelling and therefore before the follicles are suspected of having any progesterone content. In certain bats the follicles which are present at the time of the autumnal heat are even less developed. According to Courrier (22) they do not contain follicular fluid and according to Guthrie (33) and Guthrie and Jeffers (38), the follicle which is respon-

sible for the heat induced in the fall has only a small antrum and is not even intermediate in size. As before, however, such morphological studies are not sufficient to give finality to the conclusion they suggest. Until the hormonal output of the ovaries at the time of heat is known, and until replacement therapies have been attempted in spayed individuals, decision must be withheld.

Not all the attempts to induce estrous behavior artificially have involved injections of ovarian hormones into spayed animals. Following the discovery of the importance of the gonadotrophic hormones for ovarian function by Smith and Engle, and Zondek and Aschheim (Smith, 39; Fevold, 39; Engle, 39), numerous tests of their morphological and physiological action on intact animals were accompanied by observations of mating behavior. Data bearing on the action of these hormones have been accumulated for prepuberal rats (Mahnert, 30; Cole, 36, 37), constant estrous rats (Witschi and Pfeiffer, 35; Ball, 36a), hypophysectomized rats (Evans, Meyer and Simpson, 33; Liu and Noble, 39), prepuberal mice (Mirskaya and Crew, 30; Wiesner and Mirskaia, 30), diestrous guinea pigs (Dempsey, Hertz and Young, 36), prepuberal rabbits (Mahnert, 30), anestrus sheep (Cole and Miller, 33, 35; McKenzie and Terrill, 37), normal mares (Catchpole, 35; Zavadowsky and Goldberg, 37; Neves e Castro, 38), anestrus ferrets (Hill and Parks, 30), anestrus and metestrus dogs (Swingle, Parkins, Taylor, Hays and Morrell, 37; Leatham, 38; Leatham and Morrell, 38, 39), and anestrus cats (Friedgood, 39; Windle, 39). In general, the expectation that these substances injected into prepuberal, anestrus, diestrous or hypophysectomized individuals would induce mating responses through their action on the ovaries, has been realized. In certain

experiments the percentage of animals in which heat was induced was small (Hill and Parkes, 30; Mahnert, 30; Mirskaya and Crew, 30; Wiesner and Mirskaia, 30; McKenzie and Terrill, 37). In at least two experiments the period of heat was considerably shorter than that displayed normally (McKenzie and Terrill, 37; Dempsey, Hertz and Young, 36). Such irregularities indicate that the optimal dosage and method of administration were not always found. On the other hand, results with the dog were more successful in that the experimentally induced heat periods were similar to those seen in normal estrous animals. Such being the case, the gonadotrophic hormones must have been administered in such a way that their normal manner of action on the ovaries was approximated.

From an economic standpoint this method of inducing heat may be of considerable value. As a means to a better understanding of the factors which are responsible for the induction of heat, it will be of greater value when the precise part played by each gonadotrophic hormone in producing the ovarian hormones is known. So long as the injection of an apparently pure follicle-stimulating substance is sometimes followed by luteinization (Foster and Fevold, 38; Saunders and Cole, 38), and the injection of the luteinizing fraction is sometimes followed by follicular growth (Leatham and Morrell, 39), the administration of these hormones to intact animals does not give as reliable an indication of the hormones directly involved in the induction of heat as the administration of purified ovarian hormones to spayed animals.

Other endocrine factors

There is no evidence that endocrine organs other than the ovaries have any direct rôle in the induction of estrus. A

sufficiently high percentage of hypophysectomized animals have mated following the administration of estrogenic substances to exclude the possibility that secretions of this gland are necessary beyond their action as gonadotrophic agents. Robson and Schönberg (37) report that two hypophysectomized rabbits injected with triphenyl ethylene mated, and according to Sammartino and Arenas (39), hypophysectomized spayed dogs displayed the behavior of heat after being injected with 200 I.U. or more estradiol benzoate for 15 to 87 days. Maes (40a) was quite successful with hypophysectomized cats, 7 of 8 responding to 10,000 I.U. estradiol benzoate after an interval of 2 to 5 days. Early attempts to induce heat in hypophysectomized rats failed (Ball, 36a), but results reported more recently were positive (Ball, 41). Dempsey (39) did not obtain any response following the injection of estrogen and progesterone into 7 hypophysectomized guinea pigs, although 3 spayed animals from which the hypophysis had not been completely removed responded normally. The reviewer attributes Dempsey's failure to the severe general effects of this operation on the guinea pig rather than to the possibility that the action of estrogen and progesterone must be supplemented by some secretion from the pituitary.

Although the direct participation of hypophyseal hormones in the induction of estrus seems unlikely, a certain regulatory action on the length of heat is indicated by data obtained from a variety of species. In the guinea pig (Young, Dempsey, Myers and Hagquist, 38), the ewe (Quinlan and Maré, 31), the cow (Williams and Williams, 21), the mare Schtschjekin, 30; Hammond, 34; Mirskaia, 35; McKenzie and Andrews, 37; Neves e Castro, 38; Day, 39b, 40), the cat (Liche, 39), and the ferret (Marshall, 04a, 04b;

Robinson, 18; Hammond and Marshall, 30), the length of heat seems determined in part by the time required for ovulation to occur. Since structural conditions in the ovaries of guinea pigs which were examined could be excluded from having such an effect, the manner of hypophyseal action resulting in ovulation has been postulated to be important (Young, Dempsey, Myers and Hagquist, 38). Obviously this statement leaves much to be explained and proved, but in the opinion of the reviewer it indicates another direction toward which we must look for the identification of the factors which determine the character of heat.

The effects of adrenalectomy and thyroidectomy on the vaginal condition or activity have received some attention, but the rôle of these and the other glands of internal secretion on the induction of mating responses has been but little studied. It is only known that adrenalectomized female rats which ultimately died of adrenal insufficiency mated soon after the operation (Tobin, 40). With norms of behavior now established for the rat and guinea pig (Hemmingsen, 33; Ball, 37a; Blandau, Boling and Young, 41; Young, Dempsey and Myers, 35b; Young, Dempsey, Myers and Hagquist, 38; Young, Dempsey, Hagquist and Boling, 39), a more comprehensive investigation of the relationship between these important endocrines and mating behavior would be of interest.

The ovarian condition

Only when abnormalities exist which interfere with the regularity of follicle growth or ovulation, or when abnormalities occur as a consequence of defective hypophyseal function, does there seem to be an effect on mating behavior. The injuries caused by X-irradiation (Parkes, 26, 27a; Genther, 31, 34) or traumatiza-

tion (Wang and Guttmacher, 27; Ball, 34b; Lipschütz, 37, 38) are abnormalities of the first type. In Parkes' and Genther's experiments heat was displayed by many animals, but despite the implication given by Parkes (27b) that essentially normal cycles occurred, the reviewer feels that irregularities were shown in the length of heat and cycle which represent an effect of ovarian injury.

The failure of ovulation and development of persistent cystic follicles is an abnormality of the second type. In the lower mammals this condition has been described for the rat (Hemmingsen and Krarup, 37b), guinea pig (Courrier, 25) rabbit (Harris, 37), ewe (Grant, 34), cow (Pearl and Surface, 15; Williams and Williams, 21) and horse (Williams and Williams, 21). It is said to be responsible for nymphomania and even the assumption of secondary male sex characters in the cow, for nymphomania in the rabbit and horse, to result in constant estrus in the rat—a state which the reviewer assumes is analogous with the nymphomaniac condition of cows and horses, and to be without effect in the ewe. The behavior of the guinea pig studied by Courrier (25) was not observed, but the prolonged, intermittent estrus in this species (Young, Dempsey, Myers and Hagquist, 38) is thought attributable to a delay in ovulation, and to represent an approach to constant estrus.

In other respects, the ovarian condition apparently can vary within rather broad limits without influencing the cyclic appearance or character of heat. In sheep (Marshall, 04a, McKenzie and Terrill, 37) and guinea pigs (Young, Dempsey, Myers and Hagquist, 38) no relationship exists between the number of maturing follicles and the length of heat, provided one ruptures. The length of heat is likewise not affected in guinea pigs by variations

in the extent of general follicular development, provided some growing follicles are present, or in the extent of rete cyst formation, provided some ovarian parenchyma is present. In the rabbit no close relationship exists between the number and size of follicles and estrus. Büttner and Wienert (35) have observed animals which refuse the buck continuously when many large, intact follicles are present and others which accept the buck immediately and ovulate easily when only a few are present.

No ovarian condition has been found which could account for the mounting activity which is displayed by the rat (Beach, 38b). In the guinea pig no relationship exists between the extent of general follicular development or rete cyst size and the frequency of mounting. The average number of ruptured follicles was higher in animals in which mounting activity was greatest, but the significance of this observation has yet to be explained (Young, Dempsey, Myers and Hagquist, 38). The prolonged periods of mounting activity displayed by nymphomaniac cows are assumed to be a normal accompaniment of the prolonged heat and not to be attributable to any special secretions of the cystic follicles. For mounting activity as for heat the conclusion reached by Young, Dempsey, Myers and Hagquist seems valid. "... the ovary is largely an intermediary, on the one hand responding to and reflecting the character of stimuli from the hypophysis, and on the other, possessing a potentiality of action which is limited by the responsiveness of the soma upon which its secretions act."

Neural factors

Participation of the nervous system in the induction and display of mating behavior has long been assumed. Indirect evidence was given by observations on the

close relationship between seasonal changes in the daylight ration and reproductive activity (Baker and Ranson, 32; Bissonnette, 32; Bissonnette and Csech, 37; Whitaker, 36) and on the close relationship between the approach of darkness and the onset of heat (Dempsey, Myers, Young and Jennison, 34; Browman, 37; Hemmingsen and Krarup, 37b; Beach, 38a). Dependence on the nervous pathways for conduction of the light stimulus, is indicated by the delay or failure in the appearance of heat following transection of the optic nerves in ferrets (Clark, McKeown and Zuckerman, 39). Other indirect evidence for nervous system participation in the control of heat is adduced from the action of copulation in shortening heat in the rabbit, cat and ferret.

Direct evidence that nervous centers mediate the estrous responses has only recently been given (Bard, 35, 39; Brooks, 37; Fisher, Magoun and Ranson, 38; Dempsey and Rioch, 39; Dey, Fisher, Berry and Ranson, 40; Brookhart, Dey and Ranson, 40, 41). It had previously been shown that heat periods recur in the dog following transection of the cord craniad to the spinal origin of the sympathetic nervous system (Sherrington, 06), in the rabbit following complete removal of the sympathetic chains (Brooks, 38), in abdominally sympathectomized rats Bacq, 32a, 32b), and in partially and totally sympathectomized cats (Bard, 35; Simeone and Ross, 38). Typical heat behavior was displayed by a cat during spontaneous estrus and by spayed, estrogen-injected cats after complete removal of the neocortex together with part of the rhinencephalus, a little of the striatum and the rostromedial half of each thalamus (Bard, 34, 36, 39, 40; Bard and Rioch, 37). The after-reactions of these animals though distinct and sometimes briefly frantic, were usually delayed and lacked

the vigor and nicety of execution which characterized them before the cerebral ablation (Bard, 39, 40). Destruction of the cortical area did not prevent mating in the rat (Stone, 38; Davis, 39). A cat in which the thalamus was removed bilaterally showed mating behavior, copulated and became pregnant (Dempsey and Morison, personal communication). According to Ranson (34) mating occurs in female cats with bilaterally symmetrical lesions in the tuber cinereum, lateral to or behind the infundibulum. Magoun and Bard have had several cats with somewhat comparable lesions whose responses were the same as before operation, but the marked reduction in the capacity of one of these animals to exhibit estrual behavior prompts Bard (40) to suggest that the possibility of hypothalamic involvement has not been excluded. In the rabbit estrous behavior was not abolished by concurrent destruction of the auditory and visual end-organs, removal of the olfactory bulbs and bilateral ablation of the neocortex (Brooks, 37) or by complete section of the pituitary stalk (Brooks, 38). In neither the cat nor the rabbit did denervation of the vagina and vulval region have any effect. Therefore afferent impulses from the genitalia are not involved in the induction of heat in these species (Bard, 35, 39; Brooks, 37).

In the guinea pig bilateral ablation of the neocortex and other portions of the forebrain was without effect except that the responses were more easily fatigued, possibly due to non-specific effects of the operation. Likewise, heat responses were induced in an animal following transection of the brain-stem immediately anterior to the mammillary bodies, but when a second cut was made just anterior to the superior colliculus and just behind the mammillary bodies, no further responses were shown (Dempsey and Rioch, 39).

Similar results were obtained on a cat. In the same experiments Dempsey and Rioch showed that estrual behavior can also be abolished in the guinea pig by destruction of an afferent pathway for the reflex responses which runs through the posterior quadrants of the cord, crosses in the medulla and runs through the tectum mesencephali. The experiments taken together are considered to offer circumstantial evidence that estrous behavior results from the action of the sex hormones on the central nervous system and that the anterior limit of this neural mechanism lies between the intercollicular level and the anterior limit of the mammillary bodies. Bard (40), on the other hand, induced heat in a cat after complete bilateral destruction of the posterior hypothalamus, and believes therefore that the essential region for sexual behavior lies further back in the mesencephalon. Fisher, Magoun and Ranson found that cats did not mate after destruction of the supra-optic region, and Dey, Fisher, Berry and Ranson (40) report similar results from the guinea pig. The sterility in guinea pigs with anterior hypothalamic lesions is not a result of failure of the ovaries to produce sex hormones because the animals showed cyclic cornification and failed to mate following injections of estrin and progesterone (Brookhart, Dey and Ranson, 40, 41). Nevertheless, the view that the anterior hypothalamus is the region necessary for sex behavior fails to account for the presence of heat in the guinea pig after removal of all tissue rostral to the mammillary bodies (Dempsey and Rioch, 39) and for the occurrence of estrus in Bard's cat whose lesion destroyed not only the entire posterior hypothalamus, but all of the descending hypothalamic connections as well. Additional experiments are in progress and it is probable

that these conflicting opinions will soon be resolved.

The results from a study by Maes (39, 40b) suggested a conclusion which is considerably different from those given above. Following transection of the cord at the level of the first cervical segment in eight normal estrous cats and in two spayed cats brought into heat by injection of estradiol, all except one displayed raising of the pelvis, treading and movements of the tail when tapped on the perineum. Two of the three uninjected spayed animals showed some raising of the pelvis. He concludes:

These experiments demonstrate that some components at least of the sexual behavior are short arc reflexes, comparable to the scratch-reflex, which can be elicited independently of the higher centers, but the occurrence of which depends strictly on hormonal conditions. It seems, therefore, that the existence of a hypothetical sexual center should be accepted with caution, and then not so much as a pace-maker under the influence of which unspecific activities of the spinal cord are transformed into specific sexual reactions, than as a mechanism coordinating certain independent activities pre-existing at different levels of the brain stem.

That part of Maes' conclusion in which he emphasizes the dependence of hormonal stimulation is questioned because of the response given by two of his uninjected spayed animals. Furthermore, similar responses have been obtained from ovariectomized female cats decapitated when completely anestrous and from decapitate males (Bromiley and Bard, 40; Bard, 40).

In normal animals the neural paths to the pituitary may be involved at least secondarily. In the rat they mediate certain environmental effects such as cold on the cycle (Uotila, 40; Dempsey and Uotila, 40). Following pituitary stalk section many, but not all guinea pigs and rats become acyclic (Dempsey, personal communication).

An interesting point is brought out by

Dempsey and Rioch (39) and Dempsey (39). When animals are not in heat, evading reactions are shown to the same stimuli which evoke sexual behavior when animals are in heat. Inasmuch as both responses are lost with the same lesions of the colliculi and cord, it is possible that the same centers and pathways are involved.

Beyond these efforts to identify centers and tracts which mediate mating responses little has been done. The rôle of the hormones and the nature and manner of their action on the nervous system are unknown. For species in which mating behavior is induced by the synergistic action of estrogen and progesterone, no one has suggested what the nature of the conditioning action of estrogen and the supplementary action of progesterone might be. It is not certain that all the heat responses are controlled by the same nervous mechanism. Data have been presented which suggest that in the guinea pig one mechanism may control lordosis and the willingness to mate and another the homosexual or mounting activity (Young and Rundlett, 39). Finally, it is clear from data which are presented in the following section that some individuals are more sensitive to hormones than others and that certain changes in sensitivity occur as an animal develops. It should be ascertained if this sensitivity which is so important for the character of mating behavior is, among other possibilities, an expression of the responsiveness of the neural centers to hormone action.

Sensitivity to estrogen-action

Numerous observations indicate that animals differ greatly in their sensitivity to estrogen-action and whether heat is induced by estrogen alone or by the synergistic action of estrogen and pro-

gesterone, these differences account for many of the variations displayed by normal animals and by animals following replacement therapies. This possibility was first emphasized by investigators who were depending on vaginal smears for estrogen-assays (Coward and Burn, 27; Kahnt and Doisy, 28; Marrian and Parkes, 29b; D'Amour and Gustavson, 30). Of those who have investigated mating behavior, Wiesner and Mirskaia (30) seem to have been among the first, if not the first, to suggest that individual differences in the estrogen threshold might be important for the induction of mating responses. Since then the existence of spayed rats and guinea pigs whose threshold to estrogens does much to determine the response which may be expected, has been noted by Hemmingsen (33), Hemmingsen and Krarup (37a), Boling, Young and Dempsey (38), Boling and Blandau (39) and Boling, Blandau, Rundlett and Young (41).

Of immediate interest are the factors to which differences in sensitivity to estrogens can be attributed. Seasonal influences must be considered, but the little information which exists is difficult to evaluate. Bard (40) appears to assume that a seasonal refractoriness exists to estrogenic stimulation. Cole and Miller (35), on the other hand, induced heat in anestrus ewes with a single injection of estrogen and concluded that the absence of sexual desire during the anestrus is attributable to an insufficiency of estrogen. Results from injection of animals, spayed during the breeding season, which would have served as controls are not reported. By means of injections of pregnancy urine extracts (Hill and Parkes, 30) and increased daily light ratios (Bissonnette, 32), anestrus ferrets have been induced to mate. The latter treatment has also been effective on the deer mouse (Whit-

aker, 36), and the raccoon (Bissonnette and Csech, 37). For the problem at hand, such experiments indicate only that anestrus animals can respond to heat inducing stimuli. Quantitative data which would be of value in determining whether or not the sensitivity to estrogens varies from season to season can be obtained only by injecting estrogens into these species during the anestrus.

More suggestive of possible seasonal variations in the sensitivity to estrogens are observations on the bank vole (Brambell and Rowlands, 36). At the beginning of the breeding season the majority of older females experience a number of sterile cycles. Ovulation is known to occur, but there is no evidence that it is accompanied by heat. By contrast younger animals which attain puberty during the latter part of the season, frequently become pregnant at the time of the first ovulation. What is involved can only be conjectured, but on the surface a seasonal factor which influences the sensitivity of the animals to the ovarian secretions is suggested.

On the basis of mating behavior responses (Ball, 36b) and the uterine response to injected estrogens (Zuckerman, 37, 38), cyclic changes in sensitivity to estrogen-action are suggested as occurring in spayed monkeys. Inherent rhythms which are independent of ovarian action have also been postulated as being shown by the rat (Kostitch and Télérakovich, 28; del Castillo and Calatroni, 30) and guinea pig (Dempsey, 37). Consequently, the possibility that such rhythms may be associated with changes in sensitivity to estrogen must be considered. On the other hand, the consistency with which guinea pigs displayed mounting activity following repeated injections of estrogen and progesterone over a period of more than a year does not suggest any conspicu-

ous cyclic variation in the sensitivity to estrogen in this species (Young and Rundlett, 39).

Nutritional deficiencies are naturally thought of in an enumeration of the factors which modify the sensitivity to estrogen-action, especially as the lack of specific dietary requirements and undernutrition are debilitating and terminate or modify cyclic reproductive activity. Unfortunately, there is no unequivocal evidence to indicate whether or not such a relationship exists. Rats maintained on a diet deficient in vitamin E come into heat, copulate and ovulate despite their inability to retain the fetuses during the entire gestation period (Evans and Bishop, 23; Evans and Burr, 27). In several investigations involving other dietary deficiencies interference with the pituitary gonadal mechanism is indicated by the abnormal ovarian condition (Loeb, 17; Evans and Bishop, 23), or by delays in and the termination of ovulation (Osborne, Mendel and Ferry, 17; Papanicolaou and Stockard, 20; Evans and Bishop, 22; Parkes, 28; Marrian and Parkes, 29a; Guilbert and Hart, 30; Quinlan and Maré, 31; Roux, 36), but the possibility that the estrogen threshold might also have been raised has not been tested.

Conflicting opinions exist with respect to the effect of "flushing" of ewes before the beginning of the reproductive season. Grant (34) believes that flushing hastens the onset of the breeding season, not by causing an earlier production of ripe follicles, but by intensifying the secretion of estrogen or possibly by increasing the sensitivity of the receptor mechanism on which this hormone acts. Marshall and Potts (24) and Clark (34), on the other hand, state that flushing does not bring ewes into heat earlier.

The only observations which provide any direct information about the effect

of the nutritional level on the character of heat are those by McKenzie and Terrill (37). Two groups of 20 ewes each were kept on different planes of nutrition for about four and a half months. Those on the high plane gained an average of 14 pounds, and those on the low plane lost an average of 10 pounds. Nevertheless, the duration of estrus did not vary, the mean length was 25.49 hours in the former group and 25.56 hours in the latter. It is assumed from this, that under the conditions of McKenzie and Terrill's experiment, no change occurred in sensitivity to estrogen-action.

The interval between injections is considered by some to influence the vaginal response to injected estrogens (Kahnt and Doisy, 28; D'Amour and Gustavson, 30), but the few data which have been obtained in studies of behavior indicate that in the spayed rat and guinea pig the sensitivity is as great several months after a series of injections as it is only a few days later (Hemmingsen, 33; Boling, Young and Dempsey, 38). The conclusion is consistent with the point noted below that normally produced ovarian estrogens do not increase an individual's sensitivity to these hormones.

A factor to which differences in the sensitivity to estrogens can certainly be related is the age of the animal. In general the sensitivity to estrogen-action increases during the prepuberal period and probably during the first cycles in the pubescent female. Thereafter it appears to remain fairly constant for a very considerable portion of the reproductive life, after which a slight decrease may be shown. This conclusion is supported by data from intact females of several species for which the length of heat at different ages and the number of rupturing follicles are known, and by data obtained follow-

ing the injection of prepuberally spayed animals.

The heat period of the cow is slightly longer than that of the heifer (Hammond, 27). Grant (34) states that the ewes he observed varied widely in age, but none of the differences in the estrous cycle were correlated with age. McKenzie and Phillips (30) and McKenzie and Terrill (37), on the other hand, state that lambs have shorter estrous periods than older ewes, that there is no significant change between the second and eighth years of age, and that a slight decrease is shown by aged ewes. In mares 4 to 11 years, 12 to 17 years and 18 to 24 years of age the periods of heat averaged 4.38, 4.51 and 4.04 days, respectively (Constantinescu and Mauch, 36). In the guinea pig the first two heat periods tend to be shorter than those which follow. Thereafter, until about the 500th day, the average length remains approximately constant (Young, Dempsey, Myers and Hagquist, 38; Young, Dempsey, Hagquist and Boling, 39).

The ability of prepuberal animals to display mating behavior when properly stimulated is shown by the response of intact immature rats (Smith and Engle, 27; Mahnert, 30; Kraft, 32; Cole, 36, 37), mice (Smith and Engle, 27; Mirskaya and Crew, 30; Engle, 31), rabbits (Mahnert, 30), and dogs (Swingle, Parkins, Taylor, Hays and Morrell, 37; Leathem, 38) to gonadotropic hormones, and by the response of spayed immature guinea pigs to injected estrogens and progesterone (Boling, Blandau, Wilson and Young, 39). The latter authors have also described a heat-like response displayed by newborn female and male guinea pigs, but they were unable to reproduce it by hormone injections before the 20th day.

Some information has been obtained about the character of the induced heat

in prepuberal animals (Wilson and Young, 40). By the 20th day it can be induced regularly, although only when 20 R.U. estrogen are injected. Fourteen of 15 injected animals of this age displayed heat periods the length of which averaged 6.3 hours, range 1 to 11.5 hours. By the 30th day heat can be induced by injections of 10 R.U. estrogen followed by 0.1 I.U. progesterone. Its length in 14 injected animals of this age averaged 7.3 hours, range 6 to 9 hours, which is slightly longer than but not significantly different from that in spayed mature females injected similarly (Collins, Boling, Dempsey and Young, 38). The results have been interpreted to indicate that the centers responsible for heat behavior in newborn females are relatively insensitive to estrogenic stimulation, but by the 30th day in most animals a nearly normal sensitivity has been acquired.

The influences which are responsible for these changes are unknown, but supplementary observations by Wilson and Young would seem to exclude the possibility that ovarian hormones are involved. The group of 30-day old guinea pigs referred to above, was spayed within 24 hours after birth. For comparison a group of 6 was spayed between the thirtieth and thirty-fourth day and then injected with 10 R.U. estrogen followed by 0.1 I.U. progesterone. The length of heat in the first group has been noted as averaging 7.3 hours, that in the second group averaged 6.3 hours, range 6 to 7 hours. When 24 months were allowed to elapse in another group of experimental animals, the result was the same. Heat was induced promptly and its length was not different from that in the controls. Obviously removal of the gonads at the time of birth does not retard the acquisition of a sensitivity to estrogen during the first 30 days of postnatal development

or prevent retention of this sensitivity during at least a 24-month period.

When the idea of a priming action of estrogen at the time of the first heat was suggested (Young, Dempsey, Myers and Hagquist, 38), it was not suspected that the sensitivity to estrogens may develop independently. Either possibility, however, could explain the fact that the average length of initial heat periods tends to be less than that of those which occur subsequently, but the latter explanation is preferred.

Of the five factors mentioned above which conceivably could modify the sensitivity of animals to estrogenic substances, none can be held to account for the differences found in a colony of animals homogeneous with respect to age, season, availability of food and care, and yet it is under precisely these conditions that variations in threshold are shown. Apparently something more fundamental must be sought. This could be the action of one or more products of metabolism on the receptor tissues or an inherited quality of the soma. The former possibility is suggested by the observation that normal sensitivity to estrogens does not develop following the injection of androgens into female rats during the first 28 days of postnatal life (Wilson, Young and Hamilton, 40). More probable, however, is the likelihood that a genetic factor is involved. Genetic rather than gonadal factors have been postulated to have a dominant rôle in sexual differentiation during the prenatal and early postnatal periods of development (Wiesner, 34-35; Moore, 41; Wilson and Young, *in press*). That they may influence the sensitivity of the estrous behavior mechanism to estrogen is indicated by the experiments of Wilson and Young cited above, by Ball's (39) observation that male rats are more refractory to injected estrogens

than females, and by the failure of newly hatched female chicks and hens to display cock-like behavior when injected with testosterone propionate (Hamilton, 38; Hamilton and Golden, 39).

The extent to which sensitivity to estrogen-action is of importance for the problem of mating behavior in infrahuman primates does not seem to have been considered. It has recently been found that the quantity of urinary estrogens from a female chimpanzee which consistently avoids sexual contacts with males is as great as that from a normal animal studied simultaneously (Fish, Young and Dorfman, 41). Nevertheless, there is as yet no evidence that the failure of this female to mate is attributable to a low sensitivity to estrogens rather than to such non-sexual factors as social relationships or environmental circumstance. In a general way, however, differential sensitivity must exist among primates as well as among the lower mammals. If this much may be assumed, the problem is to ascertain when the failure to display sexual interest can be attributed to a low sensitivity to estrogens, when it can be attributed to social and other environmental factors, and whether or not the total picture ever involves both.

Closely related to the problem of estrogen-sensitivity is that of progesterone-sensitivity, particularly for species in which this hormone appears to be involved in the induction of mating behavior. The subject has been omitted, not because it is believed there is no variation in the threshold to this hormone, but because the possibility has received little if any attention.

Environmental influences

The influence exerted by other animals on the character of the estrous responses is greatest among the infra-human primates. Among the lower mammals, the ability

of a dominant male rat to succeed in copulation when a less aggressive animal would fail (Miller, 11; Stone, 22; Hemmingsen, 33; Ball, 37a) and the preference some ewes have for certain teasers (Roux, 36) have also been noted. On the whole, however, the character of the heat response is only slightly modified by the presence of other animals. Critical evidence that young, non-responsive mares are often brought into heat by placing them in a stall adjoining one containing a stallion or even with the male has not been found. The proximity of the bull to the cow is without stimulating action (Hammond, 27). Association with other animals, and especially those of the opposite sex, does not influence the time of sexual maturity or the normality of the first estrous responses in rats (Stone, 26) or guinea pigs (Ishii, 20; Louttit, 29). Physical maturation is of more importance for the development of reproductive behavior pattern than experience gained from association with other animals.

The character of the heat responses in domesticated and commonly used laboratory mammals is rarely influenced by handling. Wild species are entirely different. Many breed in captivity only after long periods of time and others have never been known to breed. Hartman's (23b; 39) observation that transfer of the opossum from the wild to the captive state frequently was followed by atresia of the ovarian follicles suggests that in such cases an interference with the pituitary gonadal mechanism is involved. With this much of a beginning already made, an experimental analysis of the problem would appear to be opportune.

When laboratory rodents are being handled, the behavior of the female is less easily disturbed than that of the male. In supervised breeding experiments or tests of behavior, Steinach (94) observed for the rat, Brooks (37) for the rabbit and

the reviewer for the guinea pig that copulation is usually accomplished more promptly if the female is placed with the male.

As a matter of convenience or for direct experimental purposes, reversal of the darkness-light relationship has been accomplished on the rat. Presumably heat is normal after the new rhythm is established (Hemmingsen and Krarup, 37b; Beach, 38a), although the occurrence of constant vaginal cornification in 2 of the 6 animals studied by Hemmingsen and Krarup (37b) suggests a disturbance which may be found to be reflected in the character of heat when more animals are studied. During conditions of constant darkness for a period of two months, heat ceased to be predominantly nocturnal in its occurrence in the guinea pig, but no effect was exerted on its character (Dempsey, Myers, Young and Jennison, 34).

SUMMARY

The behavior displayed at the time of estrus is described for the female mammals for which data are sufficient to permit a characterization of the species. Reasonably comprehensive information exists for the rat, guinea pig and rabbit among the rodents; sheep, cattle, pigs and horses among the ungulates; the cat and dog among the carnivores; and the howler monkey, Rhesus monkey and chimpanzee among the infrahuman primates. The generalization is warranted that each species displays a characteristic pattern of behavior within the framework of which considerable individual variation

is shown. This variation is greatest among the infrahuman primates, the circumstance being attributed to the greater plasticity of behavior in species at this phylogenetic level. In a very satisfactory number of species the behavior associated with estrus is easily identified and well adapted to investigation by quantitative methods.

In mammals which have been studied, estrous behavior has an endocrine basis. It is abolished by removal of the ovaries and restored by suitable replacement therapy. Little is known about the mechanism of hormone-action, but it appears to be mediated by a neural center or centers in the hypothalamus or even farther back in the mesencephalon. But much more is involved. Physiological factors in addition to those of endocrinal origin undoubtedly affect the character of estrus. Social and other environmental influences are assumed to be important, particularly in members of the higher Orders. Finally, individual differences that are a matter of age or differences that may be of genetic origin do much to determine the nature of the response which is shown. If any trend is evident beyond attempts to learn more about sex hormone action *per se*, it is an effort to ascertain more precisely the part played by these other factors.

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LIST OF LITERATURE

- In the text the first two digits have been omitted for the year of the reference, e.g., Cocks (1881) is shown as Cocks (81) and Aitken (1927) is shown as Aitken (27).
- AITKEN, W. A. 1927. Some observations on the oestrous cycle and reproductive phenomena of the mare. *J. Am. Vet. Med. Assoc.*, 70: 481-491.
- ALLEN, E. 1922. The oestrous cycle in the mouse. *Am. J. Anat.*, 30: 297-371.
- . 1923. Racial and familial cyclic inheritance and other evidence from the mouse concerning the cause of oestrous phenomena. *Am. J. Anat.*, 32: 293-304.
- , and DOISY, E. A. 1923. An ovarian hormone. Preliminary report on its localization, extraction

- and partial purification, and action in test animals. *J. Am. Med. Assoc.*, 81: 819-821.
- , FRANCIS, B. F., ROBERTSON, L. L., COLOATE, C. E., JOHNSTON, C. G., DOIST, E. A., KOUNTZ, W. B., and GIBSON, H. V. 1924. The hormone of the ovarian follicle; its localization and action in test animals, and additional points bearing upon the internal secretion of the ovary. *Am. J. Anat.*, 34: 133-181.
- ALTMANN, M. 1939. Behavior of the sow in relation to the sex cycle. Abstract, *Proc. Am. Physiol. Soc.*, *Am. J. Physiol.*, 126: 421.
- ARDELL, S. A., and MARSHALL, F. H. A. 1927. On the effect of the ovarian hormone in producing pro-oestrous development in the dog and rabbit. *Proc. Roy. Soc. London, Ser. B*, 101: 185-192.
- ASTWOOD, E. B. 1939. Changes in the weight and water content of the uterus of the normal adult rat. *Am. J. Physiol.*, 126: 162-170.
- AVERY, G. T. 1925. Notes on reproduction in guinea pigs. *J. Comp. Psychol.*, 5: 373-396.
- BACQ, Z. M. 1932a. The effect of sympathectomy on sexual functions, lactation, and the maternal behavior of the albino rat. With a description of the technique of sympathectomy in the rat. *Am. J. Physiol.*, 99: 444-453.
- . 1932b. Observation du comportement maternel du rat albinos sympathectomisé. *J. de Psychol. norm. et pathol.*, 28: 254-257.
- BAILEY, V. 1924. Breeding, feeding, and other life habits of meadow mice (*Microtus*). *J. Agric. Res.*, 27: 523-536.
- BAKER, J. R., and RANSON, R. M. 1932. Factors affecting the breeding of the field mouse (*Microtus agrestis*). *Proc. Roy. Soc. London, Ser. B*, 110: 313-336.
- BALL, J. 1934a. Demonstration of a quantitative relation between stimulus and response in pseudo-pregnancy in the rat. *Am. J. Physiol.*, 107: 698-703.
- . 1934b. Sex behavior of the rat after removal of the uterus and vagina. *J. Comp. Psychol.*, 18: 419-421.
- . 1936a. Further evidence on hormonal basis of "heat" behavior. *Proc. Soc. Exp. Biol. Med.*, 35: 416-418.
- . 1936b. Sexual responsiveness in female monkeys after castration and subsequent estrin administration. *Psychol. Bull.*, 33: 811.
- . 1937a. A test for measuring sexual excitability in the female rat. *Comp. Psychol. Monog.*, vol. 14, no. 1, pp. 37.
- . 1937b. Sexual responsiveness and temporally related physiological events during pregnancy in the rhesus monkey. *Anat. Rec.*, 67: 507-517.
- . 1939. Male and female mating behavior in prepubertally castrated male rats receiving estrogens. *J. Comp. Psychol.*, 28: 273-284.
- . 1940. The effect of testosterone on the sex behavior of female rats. *J. Comp. Psychol.*, 29: 151-165.
- . 1941. Mating behavior induced in hypophysectomized female rats by injected estrogen. *Proc. Soc. Exp. Biol. Med.*, 46: 669.
- , and HARTMAN, C. G. 1935. Sexual excitability as related to the menstrual cycle in the monkey. *Am. J. Obstet. Gynecol.*, 29: 117-119.
- BARD, P. 1934. On emotional expression after decortication with some remarks on certain theoretical views. Part II. *Psychol. Rev.*, 41: 424-449.
- . 1935. The effects of denervation of the genitalia on the oestral behavior of cats. Abstract, *Proc. Am. Physiol. Soc.*, *Am. J. Physiol.*, 113: 5.
- . 1936. Oestral behavior in surviving decorticate cats. Abstract, *Proc. Am. Physiol. Soc.*, *Am. J. Physiol.*, 116: 4.
- . 1939. Central nervous mechanisms for emotional behavior patterns in animals. *Res. Publ. Ass. Nerv. Ment. Dis.*, 19: 190-218.
- . 1940. The hypothalamus and sexual behavior. *Res. Publ. Ass. Nerv. Ment. Dis.*, 20: 551-579.
- , and RIOCH, D. McK. 1937. A study of four cats deprived of neocortex and additional portions of the forebrain. *Bull. Johns Hopkins Hosp.*, 60: 73-147.
- BRACH, F. A., JR. 1938a. Techniques useful in studying the sex behavior of the rat. *J. Comp. Psychol.*, 26: 355-359.
- . 1938b. Sex reversals in the mating pattern of the rat. *J. Genet. Psychol.*, 53: 329-334.
- . 1941. Execution of the complete masculine copulatory pattern by sexually receptive female rats. *J. Genet. Psychol.* (In press.)
- BINGHAM, H. C. 1928. Sex development in apes. *Comp. Psychol. Monog.*, vol. 5, no. 1, pp. 165.
- BIMONNETTE, T. H. 1932. Modification of mammalian sexual cycles; Reactions of ferrets (*Putorius vulgaris*) of both sexes to electric light added after dark in November and December. *Proc. Roy. Soc. London, Ser. B*, 110: 322-336.
- , and CATCH, A. G. 1937. Modification of mammalian sexual cycles. VII. Fertile matings of raccoons in December instead of February induced by increasing daily periods of light. *Proc. Roy. Soc. London, Ser. B*, 122: 246-254.
- BLANDAU, R. J., JORDAN, E. S., and SODERWALL, A. L. 1940. Post-parturitional heat and the time of ovulation in the albino rat. Abstract, *Proc. Am. Soc. Zool.*, *Anat. Rec.*, 78 (Suppl.): 58.

- , BOLING, J. L., and YOUNG, W. C. 1941. The length of heat in the albino rat as determined by the copulatory response. *Anat. Rec.*, 79: 453-463.
- BOLING, J. L., YOUNG, W. C., and DEMPSEY, E. W. 1938. Miscellaneous experiments on the estrogen-progesterone induction of heat in the spayed guinea-pig. *Endocrin.*, 23: 182-187.
- , and BLANDAU, R. J. 1939. The estrogen-progesterone induction of mating responses in the spayed female rat. *Endocrin.*, 25: 359-364.
- , BLANDAU, R. J., WILSON, J. G., and YOUNG, W. C. 1939. Post-parturitional heat responses of newborn and adult guinea pigs. Data on parturition. *Proc. Soc. Exp. Biol. Med.*, 42: 128-132.
- , BLANDAU, R. J., SODERWALL, A. L., and YOUNG, W. C. 1941. Growth of the Graafian follicle and the time of ovulation in the albino rat. *Anat. Rec.* 79: 313-331.
- , BLANDAU, R. J., RUNDLETT, B., and YOUNG, W. C. 1941. Factors underlying the failure of cyclic mating behavior in the albino rat. *Anat. Rec.*, 80: 155-171.
- BOURG, R. 1931. Recherches sur l'histophysiologie de l'ovaire, du testicule et des tractus génitaux du rat et de la souris. Folliculine et gravidine. *Arch. de Biol.*, 41: 245-341.
- BRAMBELL, F. W. R. 1935. Reproduction in the common shrew (*Sorex araneus* Linnaeus). I. The oestrous cycle of the female. *Phil. Trans. Roy. Soc. London*, Ser. B, 225: 1-49.
- , and HALL, K. 1936. Reproduction of the lesser shrew (*Sorex minutus* Linnaeus). *Proc. Zool. Soc. London*, 957-969.
- , and —. 1939. Reproduction of the field vole, *Microtus agrestis hirtus* Bellamy. *Proc. Zool. Soc. London*, Ser. A, 109: 133-138.
- , and ROWLANDS, I. W. 1936. Reproduction of the bank vole (*Evotomys glareolus*, Schreber). 1. The oestrous cycle of the female. *Phil. Trans. Roy. Soc. London*, Ser. B, 226: 71-97.
- BROMILEY, R. B., and BARD, P. 1940. A study of the effect of estrin on the responses to genital stimulation shown by decapitate and decerebrate female cats. Abstract, *Proc. Am. Physiol. Soc.*, *Am. J. Physiol.*, 129: P318.
- BROOKHART, J. M., DEY, F. L., and RANSON, S. W. 1940. Failure of ovarian hormones to cause mating reactions in spayed guinea pigs with hypothalamic lesions. *Proc. Soc. Exp. Biol. Med.*, 44: 61-64.
- , —, and —. 1941. The abolition of mating behavior by hypothalamic lesions in guinea pigs. *Endocrin.*, 28: 561-565.
- BROOKS, C. McC. 1937. The rôle of the cerebral cortex and of various sense organs in the excitation and execution of mating activity in the rabbit. *Am. J. Physiol.*, 120: 544-553.
- . 1938. A study of the mechanism whereby coitus excites the ovulation-producing activity of the rabbit's pituitary. *Am. J. Physiol.*, 121: 157-177.
- BROWMAN, L. G. 1937. Light in its relation to activity and estrous rhythms in the albino rat. *J. Exp. Zool.*, 75: 375-388.
- BÜTTNER, W., and WIERNERT, K. 1935. Dauerbrunst und Follikelpersistenz. (Experimentelle Untersuchungen an Kaninchen.) *Arch. Gynäk.*, 159: 64-83.
- CARPENTER, C. R. 1934. A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Monog.*, vol. 10, no. 2, pp. 163.
- . 1935. Behavior of red spider monkeys in Panama. *J. Mammal.*, 16: 171-180.
- . 1942. Sexual behavior of free ranging Rhesus monkeys (*Macaca mulatta*). I. Specimens, procedures and behavioral characteristics of estrus. *J. Comp. Psychol.* (In press.)
- . 1942. Sexual behavior of free ranging Rhesus monkeys (*Macaca mulatta*). II. Periodicity of estrus, homosexual, autoerotic and non-conformist behavior. *J. Comp. Psychol.* (In press.)
- DEL CASTILLO, E. B., and CALATRONI, C. J. 1930. Cycle sexuel périodique et folliculine. *Compt. rend. Soc. Biol.*, 104: 1024-1028.
- CATCHPOLE, H. R. 1935. Increasing breeding efficiency on stud farms through pregnancy diagnosis. *Ver. J.*, 90: 493-498.
- CHAPMAN, A. B., and CASIDA, L. E. 1937. Analysis of variation in the sexual cycle and some of its component phases, with special reference to cattle. *J. Agric. Res.*, 54: 417-435.
- CLARK, R. T. 1934. Studies on the physiology of reproduction in the sheep. I. The ovulation rate of the ewe as affected by the plane of nutrition. *Anat. Rec.*, 60: 125-134.
- CLARK, W. E. L., MCKEOWN, T., and ZUCKERMAN, S. 1939. Visual pathways concerned in gonadal stimulation in ferrets. *Proc. Roy. Soc. London*, Ser. B, 126: 449-468.
- COCKS, A. H. 1881. Note on the breeding of the otter. *Proc. Zool. Soc. London*, 249-250.
- COLE, H. H. 1930. A study of the mucosa of the genital tract of the cow, with special reference to the cyclic changes. *Am. J. Anat.*, 46: 261-301.
- . 1936. On the biological properties of mare gonadotropic hormone. *Am. J. Anat.*, 59: 299-331.
- . 1937. Superfecundity in rats treated with mare gonadotropic hormone. *Am. J. Physiol.*, 119: 704-712.

- , and MILLER, R. F. 1933. Artificial induction of ovulation and oestrus in the ewe during anoestrus. *Am. J. Physiol.*, 104: 165-171.
- , and —. 1935. Changes in the reproductive organs of the ewe with some data bearing on their control. *Am. J. Anat.*, 57: 39-97.
- COLLINS, V. J., BOLING, J. L., DEMPSEY, E. W., and YOUNG, W. C. 1938. Quantitative studies of experimentally induced sexual receptivity in the spayed guinea-pig. *Endocrin.*, 23: 188-196.
- CONSTANTINESCU, G. K., and MAUCH, A. 1936. Untersuchungen über das Sexualleben der Stuten. *Annal. Inst. Nat. Zootech. Roumanie*, 5: 9-78.
- CORNER, G. W. 1919. On the origin of the corpus luteum of the sow from both granulosa and theca interna. *Am. J. Anat.*, 26: 117-183.
- . 1921. Cyclic changes in the ovaries and uterus of the sow, and their relation to the mechanism of implantation. *Carn. Inst. Wash., Contr. to Embryol.*, 13: 117-146.
- COURRIER, R. 1922. Le cycle génital de la femelle chez certains mammifères hibernants. *Compt. rend. Soc. Biol.*, 87: 1365-1367.
- . 1925. Nymphomanie et ovaries kystiques. *Compt. rend. Soc. Biol.*, 93: 674-675.
- , and GROS, G. 1933. Données complémentaires sur le cycle génital de la chatte. *Compt. rend. Soc. Biol.*, 144: 275-277.
- COWARD, K. H., and BURN, J. H. 1927. The variation in the unit of the oestrus-producing hormone. *J. Physiol.*, 63: 270-279.
- CRAWFORD, M. P. 1940. The relation between social dominance and the menstrual cycle in female chimpanzees. *J. Comp. Psychol.*, 30: 483-513.
- CREW, F. A. E., and MIRSKALA, L. 1930. Mating during pregnancy in the mouse. *Nature, London*, 125: 564.
- D'AMOUR, F. E., and GUSTAVSON, R. G. 1930. A critical study of the assay of female sex hormone preparations. *J. Pharm. Exp. Therap.*, 40: 473-484.
- DANTCHAKOFF, V. 1938. Rôle des hormones dans la manifestation des instincts sexuels. *Compt. rend. Acad. Sci. Paris*, 201: 945-947.
- DAVIS, C. D. 1939. The effect of ablations of neocortex on mating, maternal behavior and the production of pseudopregnancy in the female rat and on copulatory activity in the male. *Am. J. Physiol.*, 127: 374-380.
- DAWSON, A. B., and FRIEDGOOD, H. B. 1940. The time and sequence of preovulatory changes in the cat ovary after mating or mechanical stimulation of the cervix uteri. *Anat. Rec.*, 76: 411-429.
- DAY, F. T. 1939a. Ovulation and the descent of the ovum in the fallopian tube of the mare after treatment with gonadotrophic hormones. *J. Agric. Sci.*, 29: 459-469.
- . 1939b. The oestrous cycle of the mare following removal of the foetus at various stages of pregnancy. *J. Agric. Sci.*, 29: 470-475.
- . 1940. Clinical and experimental observations on reproduction in the mare. *J. Agric. Sci.*, 30: 244-261.
- DEANERLY, R. 1938. The reproductive cycle of the golden hamster (*Cricetus auratus*). *Proc. Zool. Soc. London, Ser. A*, 108: 31-37.
- , and PARKES, A. S. 1933. The reproductive processes of certain mammals. IV. The oestrous cycle of the grey squirrel (*Sciurus carolinensis*). *Phil. Trans. Roy. Soc. London, Ser. B*, 222: 47-78.
- DEMPSEY, E. W. 1937. Follicular growth rate and ovulation after various experimental procedures in the guinea pig. *Am. J. Physiol.*, 120: 126-132.
- . 1939. The relationship between the central nervous system and the reproductive cycle in the female guinea pig. *Am. J. Physiol.*, 126: 758-765.
- , MYERS, H. I., YOUNG, W. C., and JENNISON, D. B. 1934. Absence of light and the reproductive cycle in the guinea pig. *Am. J. Physiol.*, 109: 307-311.
- , HERTZ, R., and YOUNG, W. C. 1936. The experimental induction of oestrus (sexual receptivity) in the normal and ovariectomized guinea pig. *Am. J. Physiol.*, 116: 201-209.
- , and RIOCH, D. McK. 1939. The localization in the brain stem of the oestrous responses of the female guinea pig. *J. Neurophysiol.*, 2: 9-18.
- , and UOTILA, U. U. 1940. The effects of pituitary stalk section upon reproductive phenomena in the female rat. *Endocrin.*, 27: 573-579.
- DEY, F. L., FISHER, C., BERRY, C. M., and RANSON, S. W. 1940. Disturbances in reproductive functions caused by hypothalamic lesions in female guinea pigs. *Am. J. Physiol.*, 129: 39-46.
- DODDS, E. C., LAWSON, W., and NOBLE, R. L. 1938. Biological effects of the synthetic oestrogenic substance 4:4'-dihydroxy- α : β -diethylstilbene. *Lancet*, 234: 1389-1391.
- DRAPER, R. L. 1920. The prenatal growth of the guinea-pig. *Anat. Rec.*, 18: 369-392.
- DUYVENÉ DE WIT, J. J. 1938. Ein neuer Test zum qualitativen und quantitativen Nachweis des Corpus luteum-Hormons. *Klin. Wochens.*, 17: 660-663.
- ELDER, J. H., and YERKES, R. M. 1936. The sexual cycle of the chimpanzee. *Anat. Rec.*, 67: 119-143.
- ELLIOTT, H. W. 1884. The Habits of the Fur Seal. The Fisheries and Fishery Industries of the United States; Section 1, Natural History of Useful Aquatic Animals; Part 1, Mammals; pp. 75-113.

- EMERY, F. E., and SCHWABE, E. L. 1936. The vaginal smears of rats as influenced by frequent examinations. *Anat. Rec.*, 64: 147-154.
- ENDERS, R. K. 1940. Ovulation in the mink (*Mustela vison*). Abstract, Proc. Am. Assoc. Anat., *Anat. Rec.*, 76 (Suppl. 2): 20.
- ENGLE, E. T. 1931. The pituitary-gonadal relationship and the problem of precocious sexual maturity. *Endocrin.*, 15: 405-420.
- . 1939. Gonadotropic substances of blood, urine and other body fluids. In *Sex and Internal Secretions* (edited by Edgar Allen, C. H. Danforth and E. A. Doisy), Baltimore, pp. 1003-1044.
- EVANS, H. M. 1928. The effects of inadequate vitamin A on the sexual physiology of the female. *J. Biol. Chem.*, 77: 651-654.
- , and BISHOP, K. S. 1922. On the relations between fertility and nutrition. II. The ovulation rhythm in the rat on inadequate nutritional regimes. *J. Met. Res.*, 1: 335-356.
- , and —. 1923. The production of sterility with nutritional regimes adequate for growth and its cure with other foodstuffs. *J. Met. Res.*, 3: 233-316.
- , and BURR, G. O. 1927. The antisterility vitamin E soluble. *Mem. Univ. Calif.*, 8: 1-176.
- , and COLE, H. H. 1931. An introduction to the study of the oestrous cycle in the dog. *Mem. Univ. Calif.*, 9: 65-118.
- , MEYER, K., and SIMPSON, M. E. 1933. The growth and gonad-stimulating hormones of the anterior hypophysis. *Mem. Univ. Calif.*, 11: 1281-299.
- FREE, A. R., and PARKES, A. S. 1929. Studies on ovulation. I. The relation of the anterior pituitary body to ovulation in the rabbit. *J. Physiol.*, 67: 383-388.
- , and —. 1930. Studies on ovulation. III. Effect of vaginal anaesthesia on ovulation in the rabbit. *J. Physiol.*, 70: 385-388.
- FELLNER, O. O. 1932. Schollenbildung, Brunst und Menstruation. *Arch. f. Gynäk.*, 148: 287-350.
- FEVOLD, H. L. 1939. Follicle stimulating and luteinizing hormones of the anterior pituitary. In *Sex and Internal Secretions* (edited by Edgar Allen, C. H. Danforth and E. A. Doisy), Baltimore, pp. 966-1002.
- FISH, W. R., YOUNG, W. C., and DORFMAN, R. I. 1941. Excretion of estrogenic and androgenic substances by female and male chimpanzees with known mating behavior records. *Endocrin.*, 28: 585-592.
- FISHER, C., MAGOON, H. W., and RANSON, S. W. 1938. Dystocia in diabetes insipidus. The relation of pituitary oxytocin to parturition. *Am. J. Obstet. Gynecol.*, 36: 1-9.
- FOSTER, M. A., and FEVOLD, H. L. 1938. The interrelationship of the pituitary gonadotropic hormones in follicular development and ovulation of the juvenile rabbit. *Am. J. Physiol.*, 121: 625-632.
- FOX, H. 1929. The birth of two anthropoid apes. *J. Mammal.*, 10: 37-51.
- FREI, W., and LUTZ, E. 1929. Der heutige Stand der Forschungen über das Oestrushormon und die Nymphomanie des Rindes. *Virchow's Arch. f. path. Anat.*, 271: 572-622.
- FRERE, A. G. 1929. Breeding habits of the common mongoose (*Herpestes edwardsi*). *J. Bombay Nat. Hist. Soc.*, 33: 426-428.
- FRIEDGOOD, H. B. 1939. Induction of estrous behavior in anestrus cats with the follicle-stimulating and luteinizing hormones of the anterior pituitary gland. *Am. J. Physiol.*, 126: 229-233.
- FRIEDMAN, M. H. 1938. Criteria for the selection of estrous rabbits. The significance of seasonal factors. *Endocrin.*, 22: 354-359.
- GEAR, H. S. 1926. The oestrous cycle of the baboon. *So. African J. Sci.*, 23: 706-712.
- GENTHER, I. T. 1931. Irradiation of the ovaries of guinea-pigs and its effect on the oestrous cycle. *Am. J. Anat.*, 48: 99-137.
- . 1934. X-irradiation of the ovaries of guinea pigs and its effect on subsequent pregnancies. *Am. J. Anat.*, 55: 1-45.
- GILLMAN, J. 1939. Some facts concerning the social life of Chacma baboons in captivity. *J. Mammal.*, 20: 178-181.
- GRANT, R. 1934. Studies on the physiology of reproduction in the ewe. I. The symptoms, periodicity and duration of oestrus. II. Changes in the vagina and cervix. III. Gross changes in the ovaries. *Trans. Roy. Soc. Edin.*, 58: 1-47.
- GREEN, W. W., and WINTERS, L. M. 1935. Studies on the physiology of reproduction in the sheep. III. The time of ovulation and rate of sperm travel. *Anat. Rec.*, 61: 457-469.
- GREULICH, W. W. 1934. Artificially induced ovulation in the cat (*Felis domesticus*). *Anat. Rec.*, 58: 217-224.
- GUILBERT, H. R., and HART, G. H. 1930. Some effects of varying calcium and phosphorus intake on the estrus cycle and reproduction in the rat. *Hilgardia*, 5: 101-118.
- GUTHRIE, M. J. 1933. The reproductive cycles of some cave bats. *J. Mammal.*, 14: 195-216.
- , and JEFFERS, K. R. 1938. Growth of follicles in the ovaries of the bat *Myotis lucifugus lucifugus*. *Anat. Rec.*, 71: 477-496.

- GUYÉNOT, E., PONS, K., and WISTRZYKOWSKA, J. 1932. Lutéinisation de l'ovaire et masculinisation chez le cobaye. *Compt. rend. Acad. Sci. Paris*, 194: 1051-1053.
- HAMILTON, G. V. 1914. A study of sexual tendencies in monkeys and baboons. *J. Animal Behav.*, 4: 295-318.
- HAMILTON, J. B. 1938. Precocious masculine behavior following administration of synthetic male hormone substance. *Endocrin.*, 23: 53-57.
- , and GOLDEN, W. R. C. 1939. Responses of the female to male hormone substances. With notes on the behavior of hens and newly-hatched female chicks. *Endocrin.*, 25: 737-748.
- HAMLETT, G. W. D. 1939. Reproduction in American monkeys. I. Estrous cycle, ovulation and menstruation in Cebus. *Anat. Rec.*, 73: 171-187.
- HAMMOND, J. 1927. The Physiology of Reproduction in the Cow. *Cambridge*.
- . 1934. Quelques progrès nouvellement faits dans la science relative à la reproduction des chevaux. *16th Congress Internat. d'Agricul., Budapest*, Section 6: 1-7.
- , and MARSHALL, F. H. A. 1925. Reproduction in the rabbit. *London*.
- , and —. 1930. Oestrus and pseudo-pregnancy in the ferret. *Proc. Roy. Soc. London, Ser. B*, 105: 607-630.
- , and WALTON, A. 1934. Notes on ovulation and fertilisation in the ferret. *J. Exp. Biol.*, 11: 307-319.
- HARRIS, G. W. 1937. The induction of ovulation in the rabbit, by electrical stimulation of the hypothalamohypophysial mechanism. *Proc. Roy. Soc. London, Ser. B*, 122: 374-394.
- HARTMAN, C. G. 1923a. The oestrous cycle in the opossum. *Am. J. Anat.*, 32: 353-421.
- . 1923b. Sterility of animals under changed condition. Abstract, *Am. Soc. Zool., Anat. Rec.*, 24: 394.
- . 1925. Hysterectomy and the oestrous cycle in the opossum. *Am. J. Anat.*, 35: 25-29.
- . 1928. The period of gestation in the monkey, *Macacus rhesus*, first description of parturition in monkeys, size and behavior of the young. *J. Mammal.*, 9: 181-194.
- . 1932. Studies in the reproduction of the monkey *Macacus (Pithecius) rhesus*, with special reference to menstruation and pregnancy. *Carn. Inst. Wash., Contr. to Embryol.*, 24: 1-161.
- . 1938. Some observations on the bonnet macaque. *J. Mammal.*, 19: 468-474.
- . 1939. Ovulation, fertilization and the transport and viability of eggs and spermatozoa. In *Sex and Internal Secretions* (edited by Edgar Allen, C. H. Danforth and E. A. Doisy), *Baltimore*, pp. 630-719.
- HATFIELD, D. M. 1935. A natural history study of *Microtus californicus*. *J. Mammal.*, 16: 261-271.
- HEAPE, W. 1900. The "sexual season" of mammals and the relation of the "pro-oestrus" to menstruation. *Quart. J. Micr. Sci.*, 44: 1-70.
- HEMMINGSEN, A. M. 1929. Attempts of inducing mating instincts in spayed rats and mice with ovarian extracts. Abstract, *Proc. Am. Physiol. Soc., Am. J. Physiol.*, 90: 383.
- . 1933. Studies on the oestrus-producing hormone (oestrin). *Skand. Arch. Physiol.*, 65: 97-250.
- , and KRARUP, N. B. 1937a. The production of mating instincts in the rat with chemically well-defined oestrogenic compounds. *Det. Kgl. Danske Vidensk. Selskab., Biolog. Meddel.*, vol. 13, no. 8.
- , and —. 1937b. Rhythmic diurnal variations in the oestrous phenomena of the rat and their susceptibility to light and dark. *Det. Kgl. Danske Vidensk. Selskab., Biolog. Meddel.*, vol. 13, no. 7.
- HERTZ, R., MEYER, R. K., and SPIELMAN, M. A. 1937. The specificity of progesterone in inducing sexual receptivity in the ovariectomized guinea pig. *Endocrin.*, 21: 533-535.
- VAN HEUVERSWYN, J., COLLINS, V. J., WILLIAMS, W. L., and GARDNER, W. U. 1939. The progesterone-like activity of desoxycorticosterone. *Proc. Soc. Exp. Biol. Med.*, 41: 552-554.
- HILL, M., and PARKES, A. S. 1930. On the relation between the anterior pituitary body and the gonads. II. The induction of ovulation in the anoestrous ferret. *Proc. Roy. Soc. London, Ser. B*, 107: 39-49.
- HÖCKER, U. 1938. Beiträge zur Kenntnis der Sexualvorgänge des Karakuschs. Ein Hinblick auf die künstliche Besamung. *Kühn-Arch.*, 47: 29-77.
- ISHII, O. 1920. Observations on the sexual cycle of the guinea pig. *Biol. Bull.*, 38: 237-250.
- . 1922. Observations on the sexual cycle of the white rat. *Anat. Rec.*, 23: 311-314.
- KAHN, L. C., and DOISY, E. A. 1928. The vaginal smear method of assay of the ovarian hormone. *Endocrin.*, 12: 760-772.
- KÖHLER, W. 1926. The Mentality of Apes. Translated by Ella Winter from the second (revised) German edition. *New York*, 315-317.
- KOSTITCH, A., and TĚLÉBAKOVITCH, A. 1928. Sur un rythme vaginal chez les animaux ovariectomisés. *Compt. rend. Soc. Biol.*, 100: 51-54.
- KRAFT, R. M. 1932. The effects of the gonadal-stimulating hormone of the anterior pituitary on

- the voluntary activity, the age of maturity and the size of the litter in immature female albino rats. *Am. J. Physiol.*, 102: 355-364.
- KUN, H. 1935. Psyche und Sexualhormon. *Trudy po Dinam. Razvit.*, 10: 137-149.
- KUNDE, M. M., D'AMOUR, F. E., CARLSON, A. J., and GUSTAVSON, R. G. 1930. Studies on metabolism. VIII. The effect of estrin injections on the basal metabolism, uterine endometrium, lactation, mating and maternal instincts in the adult dog. *Am. J. Physiol.*, 95: 630-640.
- LACASSAGNE, A., and GRICOUROFF, G. 1925. A propos des phénomènes de rut provoqué, chez la lapine castrée, par injection de liquide folliculaire. *Compt. rend. Soc. Biol.*, 93: 928-930.
- LEATHER, J. H. 1938. Experimental induction of estrus in the dog. *Endocrin.*, 22: 559-567.
- , and MORRELL, J. A. 1938. Gonadotropic action of normal male urine extract on the dog. *Endocrin.*, 23: 164-170.
- , and —. 1939. Induction of mating in the dog with pregnancy urine extract. *Endocrin.*, 24: 149-156.
- LEIGHT, J. A., and WICK, H. J. 1939. Diethylstilbestrol compared to estrone in causing estrus in spayed mice; and in conjunction with progestin in inducing sexual receptivity in spayed guinea pigs. *Endocrin.*, 25: 597-600.
- , —, and JEFFRIES, B. E. 1941. Percutaneous administration of estrogens followed by progestin in inducing sexual receptivity in spayed guinea pigs. *Endocrin.*, 28: 593-596.
- LEWIS, L. L. 1911. The vitality of reproductive cells. *Oklahoma Agric. Exp. Sta. Bull.*, No. 96: 3-47.
- LEWIS, W. H., and WRIGHT, E. S. 1935. On the early development of the mouse egg. *Corn. Inst. Wash., Cont. to Embryol.*, 25: 113-144.
- LICKE, H. 1939. Oestrous cycle in the cat. *Nature, London*, 143: 900.
- LIPSCHÜTZ, A. 1937. Hyperplasie expérimentale de l'endomètre avec prolifération atypique de l'épithèle utérin après des interventions ovariennes. I. Introduction. *Gynécol. et Obstétr.*, 36: 408-426.
- , 1938. Trouble de l'équilibre entre ovaire et préhypophyse. VII. Troubles latents de l'équilibre entre ovaire et préhypophyse. VIII. Réversibilité et irréversibilité des troubles sexuels. IX. Troubles intersexuels après fragmentation ovarienne complète. X. Déséquilibres préhypophysaires après d'autres interventions ovariennes. *Gynécol. et Obstétr.*, 37: 17-43.
- LIU, S. H., and NOBLE, R. L. 1939. The effects of extracts of pregnant mare serum and human pregnancy urine on the reproductive system of hypophysectomized female rats. *J. Endocrin.*, 1: 15-21.
- LOEB, L. 1914. The correlation between the cyclic changes in the uterus and the ovaries in the guinea pig. *Biol. Bull.*, 27: 1-44.
- , 1917. The experimental production of hypotypical ovaries through underfeeding. A contribution to the analysis of sterility. *Biol. Bull.*, 33: 91-115.
- LONG, J. A., and EVANS, H. M. 1922. The oestrous cycle in the rat and its associated phenomena. *Mem. Univ. Calif.*, 6: 1-148.
- LONGLEY, W. H. 1911. The maturation of the egg and ovulation in the domestic cat. *Am. J. Anat.*, 12: 139-172.
- LOUTITT, C. M. 1927. Reproductive behavior of the guinea pig. I. The normal mating behavior. *J. Comp. Psychol.*, 7: 247-263.
- , 1929. Reproductive behavior of the guinea pig. II. The ontogenesis of the reproductive behavior pattern. *J. Comp. Psychol.*, 9: 293-304.
- LOWTHER, F. DE L. 1940. A study of the activities of a pair of *Galago senegalensis moholi* in captivity, including the birth and postnatal development of twins. *Zoologica*, 25: 433-462.
- LUCAS, N. S., HUMER, E. M., and SMITH, H. H. 1927. On the breeding of the common marmoset (*Haplorhina jacchus* Linn.) in captivity when irradiated with ultra-violet rays. *Proc. Zool. Soc. London*, 447-451.
- MARR, J. P. 1939. Neural mechanism of sexual behavior in the female cat. *Nature*, 144: 598-599.
- , 1904a. Hypophysectomie et comportement sexuel de la chatte. *Compt. rend. Soc. Biol.*, 133: 92-94.
- , 1940b. Le mécanisme nerveux du comportement sexuel de la chatte. *Compt. rend. Soc. Biol.*, 133: 95-97.
- MAHNERT, A. 1930. Über die Wirkung des Vorderlappenhormons "Prolan" auf die Ovarien infantiler Nager. *Zentral. f. Gynäk.*, 54: 1730-1733.
- MARRIAN, G. F., and PARKES, A. S. 1929a. The effect of anterior pituitary preparations administered during dietary anoestrus. *Proc. Roy. Soc. London, Ser. B*, 105: 248-258.
- , and —. 1929b. The assay of oestrin. *J. Physiol.*, 67: 389-401.
- , and —. 1930. The relative amounts of oestrin required to produce the various phenomena of oestrus. *J. Physiol.*, 69: 372-376.
- MARSHALL, F. H. A. 1901. Preliminary communication on the oestrous cycle and the formation of the corpus luteum in the sheep. *Proc. Roy. Soc. London*, 68: 135-140.

- . 1904a. The oestrous cycle and the formation of the corpus luteum in the sheep. *Phil. Trans. Roy. Soc. London*, Ser. B, 196: 47-97.
- . 1904b. The oestrous cycle in the common ferret. *Quart. J. Micr. Sci.*, 48: 323-345.
- , and HAMMOND, J. 1925. The physiology of animal breeding, with special reference to the problem of fertility. *Ministry Agric. Fisheries, Res. Monograph*, No. 2., London.
- MARSHALL, F. R., and POTTS, C. G. 1924. Flushing and other means of increasing lamb yields. *U. S. Depts. Agric. Bull.*, no. 996.
- MASLOW, A. H. 1936. The rôle of dominance in the social and sexual behavior of infra-human primates: I. Observations at Vilas Park Zoo. *J. Genet. Psychol.*, 48: 261-277.
- MCKENZIE, F. F. 1926. The normal oestrous cycle in the sow. *Univ. Missouri Coll. Agric. Res. Bull.*, No. 86.
- , and PHILLIPS, R. W. 1930. Some observations on the estrual cycle in the sheep. *Proc. Am. Soc. Animal Prod.*, 138-143.
- , ALLEN, E., GUTHRIE, M. J., WARBRITTON, V., TERRILL, C. E., CASIDA, L. E., NAHM, L. J., and KENNEDY, J. W. 1933. Reproduction in the ewe. A preliminary report. *Proc. Am. Soc. Animal Prod.*, 278-281.
- , and TERRILL, C. E. 1937. Estrus, ovulation, and related phenomena in the ewe. *Univ. Missouri Coll. Agric. Res. Bull.*, No. 264.
- , and ANDREWS, F. N. 1937. Estrus and ovulation in the mare. *Proc. Am. Soc. Animal Prod.*, 64-70.
- McNUTT, G. W. 1924. The corpus luteum of the ox ovary in relation to the estrus cycle. *J. Am. Vet. Med. Assoc.*, Vol. 65, No. 5.
- MILLER, G. S., JR. 1928. Some elements of sexual behavior in primates and their possible influence on the beginnings of human social development. *J. Mammal.*, 9: 273-300.
- . 1931. The primate basis of human sexual behavior. *Quart. Rev. Biol.*, 6: 379-410.
- MILLER, N. 1911. Reproduction in the brown rat (*Mus norvegicus*). *Am. Nat.*, 45: 623-635.
- MIRSKAIA, L. M. 1935. Relation between oestrus and ovulation in the mare. *Proc. XV Internat. Physiol. Congress*, 195.
- MIRSKAYA, L. M., and CREW, F. A. E. 1930. On genital maturity in an immature soma. *J. Exp. Biol.*, 7: 248-252.
- MONTANÉ, L. 1916. A Cuban chimpanzee. *J. Animal Behav.*, 6: 330-333.
- MOORE, C. R. 1941. On the role of sex hormones in sex differentiation in the opossum (*Didelphys virginiana*). *Physiol. Zool.*, 14: 1-47.
- MYERS, H. I., YOUNG, W. C., and DEMPSEY, E. W. 1936. Graafian follicle development throughout the reproductive cycle in the guinea pig, with especial reference to changes during oestrus (sexual receptivity). *Anat. Rec.*, 65: 381-401.
- NELSON, W. O. 1929. Oestrus during pregnancy. *Science*, 70: 453-454.
- NEVES e CASTRO, A. 1938. Cycle génital chez la Jument; appétit sexuel, chaleurs, période progerminative. *Compt. rend. Soc. Biol.*, 129: 704-706.
- NICOL, T. 1933. Studies on the reproductive system in the guinea-pig; variations in the oestrous cycle in the virgin animal, after parturition, and during pregnancy. *Proc. Roy. Soc. Edin.*, 53: 220-238.
- OSBORNE, T. B., MENDEL, L. B., and FERRY, E. L. 1917. The effect of retardation of growth upon the breeding period and duration of life of rats. *Science*, 45: 294-295.
- OSLUND, R. M. 1928. Experiments with follicular and placental extracts. Abstract. *Proc. Am. Physiol. Soc.*, *Am. J. Physiol.*, 85: 398.
- PAPANICOLAOU, G. N., and STOCKARD, C. R. 1920. Effect of underfeeding on ovulation and the oestrous rhythm in guinea-pigs. *Proc. Soc. Exp. Biol. Med.*, 17: 143-144.
- PARKES, A. S. 1926. On the occurrence of the oestrous cycle after x-ray sterilisation. I. Irradiation of mice at three weeks old. *Proc. Roy. Soc. London*, Ser. B, 100: 172-199.
- . 1927a. On the occurrence of the oestrous cycle after x-ray sterilisation. II. Irradiation at or before birth. *Proc. Roy. Soc. London*, Ser. B, 101: 71-95.
- . 1927b. On the occurrence of the oestrous cycle after x-ray sterilisation. III. The periodicity of oestrus after sterilisation of the adult. *Proc. Roy. Soc. London*, Ser. B, 101: 421-449.
- . 1928. The nature of the anoestrous condition resulting from vitamin B deficiency. *Quart. J. Exp. Physiol.*, 18: 397-401.
- . 1929. The Internal Secretions of the Ovary. *London*.
- , FIELDING, U., and BRAMBELL, F. W. R. 1927. Ovarian regeneration in the mouse after complete double ovariectomy. *Proc. Roy. Soc. London*, Ser. B, 101: 328-354.
- PEARL, R., and SURFACE, F. M. 1915. Sex studies. VII. On the assumption of male secondary characters by a cow with cystic degeneration of the ovaries. *Maine Agric. Exp. Sta. Bull.*, 237: 65-80.
- QUINLAN, J., and MARÉ, G. S. 1931. The physiological changes in the ovary of the Merino

- sheep in South Africa, and their practical application in breeding. *17th Report Dir. Vet. Services and Animal Indust., Univ. of S. Africa*, pp. 663-703.
- RANKIN, S. W. 1934. The hypothalamus: Its significance for visceral innervation and emotional expression. *The Weir Mitchell Oration. Trans. Coll. Phys., Philadelphia*, 2: 222-242.
- REIN, G. 1883. Beiträge zur Kenntniss der Reifungserscheinungen und Befruchtungsvorgänge am Säugethiere. *Arch. f. Micro. Anat.*, 22: 233-270.
- REYNOLDS, S. R. M. 1931. Studies on the uterus. V. The influence of the ovary on the motility of the non-gravid uterus of the unanaesthetized rabbit. *Am. J. Physiol.*, 97: 706-721.
- , and FRIEDMAN, M. H. 1930. Studies on the uterus. III. The activity of the uterine fistula in unanaesthetized rabbits following coitus and during pseudopregnancy. *Am. J. Physiol.*, 94: 696-704.
- , and ALLEN, W. M. 1932. The effect of prostest-in-containing extracts of corpora lutea on uterine motility in the unanesthetized rabbit with observations on pseudopregnancy. *Am. J. Physiol.*, 102: 39-55.
- ROBINSON, A. 1918. The formation, rupture, and closure of ovarian follicles in ferrets and ferret-polecat hybrids, and some associated phenomena. *Trans. Roy. Soc. Edin.*, 52: 303-362.
- ROBSON, J. M. 1932. Adrenaline and the oestrous cycle in the mouse. *Proc. Roy. Soc. Edin.*, 52: 434-444.
- . 1938. Induction of oestrous changes in the monkey and bitch by triphenyl ethylene. *Proc. Soc. Exp. Biol. Med.*, 38: 153-157.
- , and HENDERSON, W. R. 1936. The action of oestrin on the bitch. *Proc. Roy. Soc. London, Ser. B*, 120: 1-14.
- , and SCHÖNBERG, A. 1937. Oestrous reactions, including mating, produced by triphenyl ethylene. *Nature, London*, 140: 196.
- ROUX, L. L. 1936. Sex physiology of sheep. *Onderstepoort J. Vet. Sci. Animal Ind.*, 6: 465-717.
- ROWLANDS, I. W., and PARKER, A. S. 1935. The reproductive processes of certain mammals. VIII. Reproduction in foxes (*Vulpes* spp.). *Proc. Zool. Soc. London*, 823-841.
- ROWLEY, J. 1929. Life history of the sea-lions on the Californian coast. *J. Mammal.*, 10: 1-36.
- SAMMARTINO, R., and ARENAS, N. 1939. Efectos de las hormonas ováricas sobre los genitales de perras enteras, castradas e hipofisoprivas. *Rev. Soc. Argent. Biol.*, 15: 131-141.
- SATO, S., and HOSHI, S. 1933. A study of reproduction in the mare. II. The study on the oestrus. *J. Jap. Soc. Vet. Sci.*, 12: 200-223.
- SAUNDERS, F. J., and COLE, H. H. 1938. On the reliability of present methods for characterizing two gonadotropic hormones, follicle-stimulator and luteinizer. *Endocrin.*, 23: 302-317.
- SCHMIDT, I. G. 1936. The excretion of theelin in the urine of guinea pigs with irradiated ovaries. *Anat. Rec.*, 64: 255-266.
- SCHTCHERKIN, V. 1930. Zur Frage der besten Methoden der Probe und Paarung der Stuten. *Tierzucht. u. Züchtungsbiol. einschl. Tierernährung.*, 18: 447-454.
- SCHULTZ, A. H., and SNYDER, F. F. 1935. Observations on reproduction in the chimpanzee. *Bull. Johns Hopkins Hosp.*, 57: 193-205.
- SEABORN, E. 1925. The oestrous cycle in the mare and some associated phenomena. *Anat. Rec.*, 30: 277-287.
- SHERINGTON, C. S. 1906. The integrative action of the nervous system. *New York*.
- SHIBATA, S. 1931. The oestrous cycle and ovulation in the rabbit. *J. Coll. Agric., Imp. Univ. Tokyo*, 11: 309-340.
- SIMEONE, F. A., and ROSS, J. F. 1938. The effect of sympathectomy on gestation and lactation in the cat. *Am. J. Physiol.*, 122: 659-667.
- SLONAKER, J. R. 1924. The effect of pubescence, oestrus and menopause on the voluntary activity in the albino rat. *Am. J. Physiol.*, 68: 294-315.
- . 1925. The effect of copulation, pregnancy, pseudopregnancy and lactation on the voluntary activity and food consumption of the albino rat. *Am. J. Physiol.*, 71: 362-394.
- . 1927. The effect of the follicular hormone on old albino rats. *Am. J. Physiol.*, 81: 325-335.
- SMITH, A. D. B. 1927a. Superfoetation—further cases in pigs and sheep. *J. Anat.*, 62: 100-104.
- . 1927b. A case of superfoetation in the pig. *J. Anat.*, 61: 329-332.
- SMITH, P. E. 1939. Effect on the gonads of ablation and implantation of the hypophysis and the potency of the hypophysis under various conditions. In *Sex and Internal Secretions* (edited by Edgar Allen, C. H. Danforth and E. A. Doisy), *Baltimore*, pp. 931-965.
- , and ENGLE, E. T. 1927. Experimental evidence regarding the role of the anterior pituitary in the development and regulation of the genital system. *Am. J. Anat.*, 40: 159-217.
- SNELL, G. D., FRETTE, E., HUMMEL, K. P., and LAW, L. W. 1940. The relation of mating, ovulation

- and the estrous smear in the house mouse to time of day. *Anat. Rec.*, 76: 39-54.
- SODERWALL, A. L. 1940. Induction of sexual receptivity in estrogen-conditioned spayed female guinea pigs by orally administered progesterone and pregnenolone. *Endocrin.*, 27: 840-841.
- , and YOUNG, W. C. 1940. The effect of aging in the female genital tract on the fertilizing capacity of guinea pig spermatozoa. *Anat. Rec.*, 78: 19-29.
- SOKOLOWSKY, A. 1923. The sexual life of the anthropoid apes. *Urol. Cut. Rev.*, 27: 612-615.
- SPIEGEL, A. 1930. Beobachtungen über den Sexualzyklus, die Gravidität und die Geburt bei Javakakaken. (*Macaca irus mordax* Thomas and Wroughton [*cynomolgus* L.]) *Arch. f. Gynäk.*, 142: 561-591.
- STEINACH, E. 1894. Untersuchungen zur vergleichenden Physiologie der männlichen Geschlechtsorgane, insbesondere der accessorischen Geschlechtsdrüsen. *Pflüger's Arch. f. d. ges. Physiol.*, 56: 304-338.
- , and KUN, H. 1931. Luteingewebe und männliche Geschlechtscharaktere. *Pflüger's Arch. f. d. ges. Physiol.*, 227: 166-178.
- STOCKARD, C. R., and PAPANICOLAOU, G. N. 1917. The existence of a typical oestrous cycle in the guinea-pig—with a study of its histological and physiological changes. *Am. J. Anat.*, 22: 225-283.
- , and —. 1919. The vaginal closure membrane, copulation, and the vaginal plug in the guinea-pig, with further considerations of the oestrous rhythm. *Biol. Bull.*, 37: 222-245.
- STONE, C. P. 1922. The congenital sexual behavior of the young male albino rat. *J. Comp. Psychol.*, 2: 95-153.
- . 1926. The initial copulatory response of female rats reared in isolation from the age of twenty days to the age of puberty. *J. Comp. Psychol.*, 6: 73-83.
- . 1938. Effects of cortical destruction on reproductive behavior and maze learning in albino rats. *J. Comp. Psychol.*, 26: 217-236.
- , and GIBB, J. 1941. The feasibility of inducing estrus in female rats for use as lures in sex research. *J. Comp. Psychol.*, 31: 297-301.
- STROTHOFF, H. 1922. Beiträge zur Sterilitätsbehandlung in Abortusbeständen. (Abortinimpfung—Eiertocksuntersuchungen.) *Arch. f. wis- sen. und prakt. Tierheilk.*, 48: 28-65.
- STRUTHERS, P. H. 1928. Breeding habits of the Canadian porcupine (*Erethizon dorsatum*). *J. Mammal.*, 9: 300-308.
- STRUVE, J. 1911. Die Perioden der Brunst bei Rindern, Schweinen und Pferden. *Fühlings Landw. Ztg.*, Jahrgang 60: 833-838.
- SVIEHLA, A. 1930. Breeding habits and young of the red-backed mouse, *Eutamias*. *Mich. Acad. Sci. Arts Letters*, 11: 485-490.
- . 1931. Life history of the Texas rice rat (*Oryzomys palustris texensis*). *J. Mammal.*, 12: 238-242.
- . 1932. A comparative life history study of the mice of the genus *Peromyscus*. *Univ. Mich. Museum Zool., Misc. Publ. No. 24*.
- , and SVIEHLA, R. D. 1931. The Louisiana muskrat. *J. Mammal.*, 12: 12-28.
- SVIEHLA, R. D. 1931. Notes on desert and dusky harvest mice (*Reithrodontomys megalotis megalotis* and *R. m. nigrescens*). *J. Mammal.*, 12: 363-365.
- SWINGLE, W. W., PARKINS, W. M., TAYLOR, A. R., HAYS, H. W., and MORRELL, J. A. 1937. Effect of oestrus (pseudopregnancy) and certain pituitary hormones on the life-span of adrenalectomized animals. *Am. J. Physiol.*, 119: 675-683.
- TINKLEPAUGH, O. L. 1928. The self-mutilation of a male *Macacus rhesus* monkey. *J. Mammal.*, 9: 293-300.
- . 1930. Occurrence of vaginal plug in a chimpanzee. *Anat. Rec.*, 46: 329-332.
- . 1933. Sex cycles and other cyclic phenomena in a chimpanzee during adolescence, maturity and pregnancy. *J. Morph.*, 54: 521-547.
- TOBIN, C. E. 1940. Pregnancy and lactation in adrenalectomized rats. Abstract, *Proc. Am. Assoc. Anat.*, *Anat. Rec.*, 76 (Suppl. 2): 55.
- TORSTVEIT, O., and MELLISH, C. H. 1941. Guinea pig copulatory reflex in response to aqueous extracts of adrenal cortex. *Proc. Soc. Exp. Biol. Med.*, 46: 239-240.
- TRENNIDER, D. B. 1922. Oestrus and fecundity in the guinea pig. *Am. Nat.*, 56: 347-359.
- TSAI, C. 1925. The relative strength of sex and hunger motives in the albino rat. *J. Comp. Psychol.*, 5: 407-415.
- UOTILA, U. U. 1940. Hypothalamic control of anterior pituitary function. *Res. Publ. Ass. Nerv. Ment. Dis.*, 20: 580-588.
- VAN DER STRICHT, R. 1911. Vitellogenèse dans l'ovule de chatte. *Arch. Biol.*, 26: 366-481.
- VOM, H. E. 1930. Der Postpartum-Oestrus der Nagetiere. *Biol. Generalis*, 6: 433-456.
- WADE, N. J., and DOHR, E. A. 1935. Cornification of vaginal epithelium of ovariectomized rats produced by smearing. *Proc. Soc. Exp. Biol. Med.*, 32: 707-709.
- WANG, G. H. 1923. The relation between 'spontaneous' activity and oestrous cycle in the white rat. *Comp. Psychol. Monog.*, Vol. 2, No. 1, pp. 27.

- . 1924. A sexual activity rhythm in the female rat. *Am. Nat.*, 58: 36-42.
- , and GUTTMACHER, A. F. 1927. The effect of ovarian traumatization on the spontaneous activity and genital tract of the albino rat, correlated with a histological study of the ovaries. *Am. J. Physiol.*, 82: 335-349.
- WARNER, L. H. 1927. A study of sex behavior in the white rat by means of the obstruction method. *Comp. Psychol. Monog.*, Vol. 4, No. 5, pp. 68.
- WATT, L. J. 1931. Ovulation, oestrus and copulation with consequent dystocia during pregnancy, in the mouse. *Science*, 73: 75-76.
- WEBER, E. 1910-1911. Untersuchungen über die Brunst des Rindes. *Arch. f. wiss. und prakt. Tierheilk.*, 37: 382-406, 442-454.
- WHITAKER, W. L. 1936. Effect of light on reproductive cycle of *Peromyscus leucopus noveboracensis*. *Proc. Soc. Exp. Biol. Med.*, 34: 329-330.
- WISNER, B. P. 1934-1935. The post-natal development of the genital organs in the albino rat. *J. Obstet. Gynec. Brit. Emp.*, 41: 867-922. 42: 8-78.
- , and MIRSKAJA, L. 1930. On the endocrine basis of mating in the mouse. *Quart. J. Exp. Physiol.*, 20: 273-279.
- WIGHT, H. M. 1931. Reproduction in the eastern skunk (*Mephitis mephitis nigra*). *J. Mammal.*, 12: 42-47.
- WILLIAMS, W. L., and WILLIAMS, W. W. 1921. The Diseases of the Genital Organs of Domestic Animals. *Ithaca*.
- WILSON, J. G., and YOUNG, W. C. 1940. The acquisition of sensitivity to estrus-inducing hormones by female guinea pigs is independent of ovarian influences. Abstract, Proc. Am. Ass. Anat., *Anat. Rec.*, 76 (Suppl. 2): 58.
- , and —. Sensitivity to estrogen studied by means of experimentally induced mating responses in the female guinea pig and rat. *Endocrin.* (In press.)
- , —, and HAMILTON, J. B. 1940. A technic suppressing development of reproductive function and sensitivity to estrogen in the female rat. *Yale J. Biol. Med.*, 13: 189-202.
- WILSON, K. M. 1926. Histological changes in the vaginal mucosa of the sow in relation to the oestrous cycle. *Am. J. Anat.*, 37: 417-431.
- WINDLE, W. F. 1939. Induction of mating and ovulation in the cat with pregnancy urine and serum extracts. *Endocrin.*, 25: 365-371.
- WITSCHI, E., and PFRIFFER, C. A. 1935. The hormonal control of oestrus, ovulation and mating in the female rat. *Anat. Rec.*, 64: 85-105.
- WOOD, F. D. 1935. Notes on the breeding behavior and fertility of *Neotoma fuscipes macrotis* in captivity. *J. Mammal.*, 16: 105-109.
- YERRES, R. M. 1939a. Sexual behavior in the chimpanzee. *Human Biol.*, 11: 78-111.
- . 1939b. Social dominance and sexual status in the chimpanzee. *Quart. Rev. Biol.*, 14: 115-136.
- . 1940. Social behavior of chimpanzees: Dominance between mates, in relation to sexual status. *J. Comp. Psychol.*, 30: 147-186.
- , and ELDER, J. H. 1936. Oestrus, receptivity, and mating in chimpanzee. *Comp. Psychol. Monog.*, Vol. 13, No. 5, pp. 39.
- YOUNG, W. C. 1937. The vaginal smear picture, sexual receptivity, and the time of ovulation in the guinea pig. *Anat. Rec.*, 67: 305-325.
- , DEMPSEY, E. W., and MYERS, H. I. 1935a. A working hypothesis concerning the cause of oestrus in the guinea pig. Abstract, Proc. Am. Assoc. Anat., *Anat. Rec.*, 61 (Suppl.): 65.
- , —, and —. 1935b. Cyclic reproductive behavior in the female guinea pig. *J. Comp. Psychol.*, 19: 313-335.
- , —, HAGQUIST, C. W., and BOLING, J. L. 1937. The determination of heat in the guinea pig. *J. Lab. Clin. Med.*, 23: 300-302.
- , —, MYERS, H. I., and HAGQUIST, C. W. 1938. The ovarian condition and sexual behavior in the female guinea pig. *Am. J. Anat.*, 63: 457-487.
- , —, HAGQUIST, C. W., and BOLING, J. L. 1939. Sexual behavior and sexual receptivity in the female guinea pig. *J. Comp. Psychol.*, 27: 49-68.
- , and RUNDLETT, B. 1939. The hormonal induction of homo-sexual behavior in the spayed female guinea pig. *Psychosomatic Med.*, 1: 449-460.
- , BOLING, J. L., and BLANDAUI, R. J. 1941. The vaginal smear picture, sexual receptivity and the time of ovulation in the albino rat. *Anat. Rec.*, 80: 37-45.
- ZAVADOWSKY, B. M., and GOLDBERG, M. B. 1937. The effect of prolane upon the sexual activity of mares. *Bull. Biol. et Méd. Expér., U. R. S. S.*, 3: 357-359.
- ZUCKERMAN, S. 1930. The menstrual cycle of the primates. I. General nature and homology. *Proc. Zool. Soc. London*, 691-754.
- . 1932. The Social Life of Monkeys and Apes. *London*.
- . 1937. Cyclical fluctuations in oestrin threshold. *Nature, London*, 139: 628.
- . 1938. The interaction of ovarian hormones in the menstrual cycle. *Actualités Sci. et Indust.*, No. 602: 121-137.



NUTRITION IN THE PROTOZOA

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AN UNDERSTANDING of the nutrition of an organism involves a knowledge of the specific substances needed and utilized by that organism in its metabolism and growth. In recent years tremendous advances have been made in the field of bacterial nutrition. Advances in protozoan nutrition have not been as rapid.

Protozoans obtain nourishment in different ways. Until recent years these were usually referred to as:

- (1) holophytic nutrition—in which the organisms carry on photosynthesis and are capable of continued growth in a suitable inorganic medium, in the presence of light;
- (2) saprozoic or saprophytic nutrition (also parasitic)—in which organic compounds in solution are required and utilized; and
- (3) holozoic nutrition—in which the organisms ingest solid organic material. This ingestion of particulate matter, in contrast with the diffusive method of obtaining nutrient requirements as found in (1) and (2), is the characteristic animal-way of obtaining food.

When the various classes of the Protozoa are considered with respect to the mode or modes of obtaining nourishment, we find that:

- (1) the three types of nutrition, holophytic, saprophytic and holozoic, occur in practically all the orders of the Mastigophora;
- (2) holozoic nutrition is almost universal in the Sarcodina, saprophytism is rare;
- (3) with the exception of certain highly modified parasitic forms, all of the Ciliata utilize solid food; and

- (4) all of the Sporozoa exhibit parasitic nutrition.

Most of the colorless free-living protozoans exhibit, wholly or in part, holozoic nutrition. In this discussion a rather brief consideration of our knowledge of holophytic and saprophytic nutrition in the Protozoa is followed by a more detailed consideration of the problems of holozoic nutrition. Why a special interest in the nutrition of holozoic forms? The nutrition of any of these types is interesting from a physiological viewpoint. From a comparative physiological viewpoint the fact that less is known about the nutrition of holozoic forms than about either the holophytic or saprozoic forms suggests that more attention should be given to this type of nutrition. Knowledge gained about the nutrition of free-living holozoic forms, as well as about the other types, may be useful in gaining an understanding of the nutrition of related parasitic forms. The rôle of protozoans in the economy of the elements in nature is little understood and a solution of some of the problems of holozoic nutrition will aid materially in this field. There is a large group of biologists who consider that certain of these holozoic protozoans are especially suited for investigations on certain fundamental problems of protoplasm and of cells, problems of cell differentiation, of heredity, of sex and others, where completely controlled conditions, both en-

vironmental and organismic, are essential to final solutions. For these workers an exact knowledge of the nutrition of these forms is quite essential. And finally, there is an interest in the study of the nutrition of these forms because of the light which the information obtained may shed on evolutionary relationships. In this connection, Sandon (1932), in his monograph *The Food of the Protozoa*, p. 1, states,

The animal kingdom presumably had its origin when some unicellular organisms, previously accustomed to nourishing themselves after the manner of plants, began to eat the bodies (either living or dead) of their neighbors. The rest of the story of the evolution of animals presents itself to us as something which follows with every appearance of inevitability and purposefulness out of this one revolutionary change. Though the earlier stages of this story may be irretrievably lost in the remote past, the unicellular organisms of the present day provide us with what we may reasonably imagine to be a very fair reconstruction of a very considerable part of it. Among the flagellates, organisms are still changing from plants into animals. Some of them can even be made to cross the boundary from one kingdom to the other under the carefully controlled conditions of a laboratory experiment. In many more cases the similarity between a colorless animal flagellate and another which contains chlorophyll is so close that the systematist includes them in the same family or even in the same genus, from which we conclude that the difference between them is a relatively recent development. From such beginnings the Protozoa—those unicellular creatures which have definitely adopted the animal way of living—show amazingly varied developments alike in morphology, in physiology and in ways of feeding. It seems hardly likely that these developments are not intimately connected with one another.

Researches of recent years by Lwoff, Dusi, Mainx, Pringsheim, Hall and others have shown that the nutrition of green forms formerly classed as holophytic or autotrophic varies, as also does the nutrition of those forms formerly classed as saprophytic or saprozoic. Hall (1939) has recently proposed a new classification of nutritional types based on the sug-

gestions of several workers. He proposes to designate the holophytic type of nutrition as *phototrophic nutrition* with the following subdivisions on the basis of the simplest possible nitrogen requirements in each case:

- (1) Photoautotrophic nutrition—characteristic of green forms which can grow in inorganic solutions, such as *Chlorogonium euchlorum*.
- (2) Photomesotrophic nutrition—exhibited by green species which are able to grow in media containing amino acids but not in inorganic media, such as *Euglena deses*.
- (3) Photometatrophic nutrition—characteristic of green forms capable of growth in peptone solutions but not in amino acids or inorganic solutions, such as *Euglena pisciformis*.

For the colorless organisms which require an organic carbon source in the absence of chlorophyll, he proposes the term *heterotrophic nutrition*. On the basis of nitrogen requirements he divides heterotrophic nutrition into the following classes:—

- (1) Heteroautotrophic nutrition—where there is the utilization of inorganic compounds of nitrogen in the presence of an organic carbon source, as in *Polytoma uvella*.
- (2) Heteromesotrophic nutrition—in which the growth requirements may be satisfied by one or more amino acids as sources of nitrogen and of carbon (growth is usually more vigorous with an additional carbon source), as in *Polytomella caeca*.
- (3) Heterometatrophic nutrition—characteristic of organisms which grow in peptone solutions but not in amino-acid media or in inorganic solutions, such as *Hyalogonium klebsii*.

A classic piece of work in the field of protozoan nutrition was that of Pringsheim (1921), who was perhaps the first to culture successfully a colorless flagellate in a sterile medium of known chemical composition. Working with *Polytoma uvella*, he found that this species could satisfactorily nourish itself with ammonium salts (sulphate or phosphate) as the only source of nitrogen and sodium

acetate or butyric acid as the carbon source. Certain amino acids could be utilized while nitrates could not. Sugars were of no nutritive value.

Lwoff and his co-workers verified this work and extended the method to other forms, emphasizing the importance of using sterile media (containing no other species of living organisms) and of knowing the chemical constitution of the media.

Numerous investigations have been made in recent years on various species of the Euglenida and of the Phytomonadida. In the light of present evidence *Euglena gracilis*, *E. klebsii* and *E. stellata* may be recognized as photoautotrophs. *E. deses* and *E. pisciformis* appear to be incapable of growth in inorganic media. *E. deses* has been grown on amino acids, whereas *E. pisciformis* apparently requires peptones. In darkness, *E. gracilis* can be grown in peptone media and is no longer dependent on photosynthesis. In a similar fashion *E. mesnili* has been grown in darkness and a strain entirely lacking chlorophyll has been maintained in the laboratory by Lwoff and Dusi (1938). On the other hand, there is no evidence that *E. anabena*, *E. deses*, *E. klebsii* and *E. pisciformis* are capable of continued growth in darkness. So in the genus *Euglena* all types of phototrophic nutrition must be recognized, and, in addition, a facultative heterotrophic type. There is a definite evolutionary trend here away from the primitive autotrophic condition.

All of the green Phytomonads investigated have photoautotrophic nutrition in the light and are capable of heteromesotrophic nutrition in darkness (e.g., *Chlamydomonas*, *Chlorogonium*, and *Haematococcus*). In the colorless Phytomonads we find a series beginning with *Polytoma uvella*, already discussed, and including *Polytomella caeca* which requires amino

acids, and *Hyalogonium klebsii* which requires peptones. In this group, also, there is a definite trend toward the more animal-like methods of nutrition.

Much, then, has been accomplished in analyzing the nutrition of protozoans which normally take in their nutritive requirements in the form of dissolved substances. But what is definitely known about the nutrition of particulate feeders or holozoic forms?

Many attempts have been made to get at this problem by culturing holozoic protozoans in sterile non-particulate media of known composition. Lwoff (1932), in his treatise on the nutrition of protozoans, states that up until that time the only holozoic form which had been cultured successfully in a purely liquid medium was the ciliate, *Glaucoma piriiformis*, originally isolated in pure culture by Lwoff in 1923.

Peters (1921) reported that he had cultured successfully the ciliate *Colpidium colpoda* in bacteria-free cultures on an ammonium-glycero-phosphate medium. Other workers tried to repeat his work without success, and in 1929 Peters reported that slow growing bacteria had been found in his cultures.

Lwoff found that nitrogen in the form of nitrates, ammonium salts, isolated amino acids, mixed amino acids, hydrolyzed silk and creptone would not maintain continued growth of *Glaucoma piriiformis* in bacteria-free cultures. However, peptones of muscle and peanut, produced either by pancreatic or peptic digestion, and yeast autolysate, supported luxuriant growth over many transfers. Lwoff found that this ciliate produces a proteolytic enzyme which hydrolyzes a part of the peptones in the medium to amino acids. But as he found that natural mixtures of amino acids (e.g., creptone) would not maintain continued growth,

he concluded that *Glaucoma* requires its nitrogen in a form no less complex than peptids, and that it actually absorbs peptones.

How does this ciliate, which normally obtains its nutrients by forming food vacuoles at the base of the cytopharynx, obtain them in a purely liquid medium? It is Lwoff's opinion that most of the peptids and peptones utilized enter directly through the pellicle. He found on the average from 1 to 5 liquid vacuoles in the *Glaucoma* examined and states that because of the rapid division of these ciliates it would not seem probable that all of the

forms which would not grow in the peptone media were obligatory particulate-feeders. However, the normally holozoic forms in the following list have been successfully grown in bacteria-free cultures, according to the various authors listed (Table 1).

There seems to be little doubt about the validity of the results in the first seven cases. Loefer's strain of *Paramecium bursaria* is undoubtedly sterile, but this case differs from the others in that it has associated with it symbiotic green algae, and he has not been able to grow this species of *Paramecium* in pure culture when

TABLE 1

Holozoic protozoans grown in pure culture

ORGANISM	AUTHOR	MEDIUM
1. <i>Glaucoma piriformis</i>	Lwoff (1923)	peptone
2. <i>Glaucoma scintillans</i>	Hetherington (1923)	peptone-glucose and yeast autolysate
3. <i>Glaucoma ficaria</i>	Johnson (1935)	tryptone
4. <i>Colpidium campylum</i>	Butterfield (1929)	peptone and yeast autolysate
<i>Colpidium campylum</i>	Hetherington (1933)	peptone-glucose and yeast autolysate
5. <i>Colpidium striatum</i>	Elliott (1933)	tryptone
6. <i>Lexoecephalus granulatus</i>	Hetherington (1933)	peptone-glucose and yeast autolysate
7. <i>Leucophrys patula</i>	Thomas (unpublished)	yeast autolysate
8. <i>Paramecium bursaria</i>	Loefer (1934)	tryptone
*9. <i>Mayorella palestinensis</i>	Reich (1935)	peptone-glucose

* This form is an amoeba—all the others are ciliates.

nutrients entered in the vacuoles formed. He states that it is not difficult to assume that these substances in the medium pass through the external membrane directly into the cytoplasm, when it is surely true that, as normal products of digestion in the vacuoles, they pass through the walls of the vacuoles into the cytoplasm. That such an assumption is reasonable is borne out by the fact that polypeptids are absorbed from the medium by *Polytoma*, *Chlamydomonas*, *Hematococcus*, and several Trypanosomes.

Lwoff attempted to cultivate several other ciliates and some amoebae in peptone media, but without success. He concluded in his 1932 monograph that these

freed of the algae. In 1930 Glaser and Coria reported the pure culture of *Trichoda* and *Chilodon cucullus* in sterile bouillon medium, but in 1935 they reported that these cultures did not thrive after numerous transfers. Thus they did not meet the critical test for pure cultures. No one, as yet, has verified the work of Reich on the amoeba, *Mayorella*.

The nitrogen requirements of all of these forms seem to be quite similar. In no case has it been possible to grow one of these forms on a single amino acid or on mixtures of amino acids. However, Elliott (1935) and Hall and Elliott (1935), working with two species of *Colpidium*, found that the best growth was obtained in those

media high in amino acid content, indicating that these ciliates do utilize amino acids.

While the peptone media support good growth of the various ciliates reported, some acceleration of growth has been reported upon the addition of carbohydrates to the media. Lwoff (1925) found that *Glaucoma piriiformis* utilizes maltose, levulose, galactose, and dextrose. Elliott (1935) reported that the two species of *Colpidium* studied were able to ferment these four sugars and in addition starch. Following the lead of v. Brand (1935), who, by the use of direct quantitative analytical methods, was able to show a difference in the rate of utilization of dextrose between several different species of Trypanosomes, Loefer (1938) was able to determine quantitatively the amount of dextrose used by cultures of *Colpidium campylum* and *Glaucoma piriiformis*. Reich states that good growth occurred in his amoeba cultures only when dextrose, levulose or lactose was supplied.

But little is known about the use of fatty acids by these forms. Bond (1933) obtained "heavy growth" of *Colpidium campylum* with sodium salts of acetic, pyruvic and tartaric acids. Elliott (1935) reported that butyric acid accelerates the growth of *Colpidium striatum* in a restricted pH range.

It is interesting to note that the first seven species listed (and on which most of the studies have been made) are members of the same family—Frontonitidae. Another interesting fact is that one of these, *Leucophrys parula*, is, at least in one stage of its life cycle, a carnivorous form. Lepsi (1926) first reported that this form passes from a small bacterial-feeder to a large carnivorous form, and recently Dr. Waldo Furgason (personal communication) has been able to verify this, and to establish the nature of the life cycle. The fact that

one carnivorous form has been grown in pure culture should be stimulating to further work of this kind.

Not many observations have been made on the exact way the nutrients are taken in by the different forms. Hetherington (1933) states, in referring to his cultures of *Colpidium campylum*, that "They are fatter than their typical condition in nature, always showing numerous food-vacuoles which are clear. Presumably they ingest the medium." Lwoff concluded that *Glaucoma piroformis* absorbs its medium to a large extent. The fact that this species of *Glaucoma* is sometimes found as a parasite in certain invertebrates and lower vertebrates (Epstein, 1926; Lwoff, 1932) might indicate that it has a greater capacity for absorbing nutrients directly through its pellicle than some of the others.

Many attempts have been made to culture numerous ciliates in sterile particle-free media, with negative results. Actually the first attempts to control the food of holozoic ciliates were made, not by the pure culture method, but by trying to culture different ciliates on single known kinds of bacteria. Many investigations on numerous protozoans have been made along this line; and, in the beginning, the purpose of such work was not so much that of understanding the nutrition of the organisms but rather that of obtaining greater control of the environment in experimental work on the organisms. Maupas (1888) and Jennings (1908) both suggested the need for such control of the food of protozoans but no real progress was made until the work of Hargitt and Fray (1917). These workers sterilized paramecia by repeated washings and then introduced them into infusions containing a single known kind of bacterium and into mixtures of several kinds. They found that *Bacillus subtilis* supported fair growth

of *Paramecium* when used alone but concluded that a mixture of several kinds formed a more suitable diet. Phillips (1922) also working with *Paramecium*, and Luck, Sheets and Thomas (1931), working with *Euplores taylori*, reached essentially the same conclusion.

Other workers, however, have been successful in culturing several ciliates on a single strain of bacteria. In this category belong the results of E. and M. Chatton (1923), who grew *Glaucoma scintillans* on

the work of this nature which has been done in the last few years. Practically all of the investigators have found that some species of bacteria are good, some only fair, and some are actually toxic, when used as the only source of food for different protozoans. However, when one goes through the literature on this subject he is impressed with the fact that the various workers have not obtained the same results when using the same species of bacteria and the same species of protozoa.

TABLE 2*

Suitability of various bacteria as food for Paramecium according to different investigators

SUITABLE	UNSUITABLE
<i>Bacillus subtilis</i>	<i>Bacillus subtilis</i>
<i>Bacillus coli</i>	<i>Bacillus coli</i>
<i>Bacillus proteus</i>	<i>Bacillus proteus</i>
<i>Bacillus cereus</i>	<i>Bacillus cereus</i>
<i>Bacillus aquatilis</i>	<i>Bacillus enteritidis</i>
<i>Bacillus lactis aerogenes</i>	<i>Bacillus Raveneli</i>
<i>Bacillus pyocyaneus</i>	<i>Bacillus prodigiosus</i>
<i>Bacillus candicans</i>	<i>Bacillus dendriticus</i>
<i>Bacillus megatherium</i>	<i>Bacillus flavescens</i>
<i>Bacillus niger</i>	<i>Bacillus fluorescens</i>
<i>Achromobacter pinnatum</i>	<i>Azotobacter</i>
<i>Erythrobacillus prodigiosus</i>	<i>Staphylococcus aureus</i>
<i>Flavobacterium brunneum</i>	<i>Aerobacter aerogenes</i>
<i>Pseudomonas fluorescens</i>	<i>Serratia marcescens</i>
<i>Pseudomonas ovalis</i>	<i>Escherichia coli</i>
	<i>Pseudomonas fluorescens</i>
	<i>Micrococcus flavus</i>
	<i>Bacterium plicatum</i>

* From Leslie, 1940b.

both *B. coli* and *B. fluorescens*; Hetherington (1933) who grew *Colpidium* on twelve different species used singly; Barker and Taylor (1931), who obtained excellent growth of *Colpoda cucullus* on *Pseudomonas fluorescens*; Johnson (1933), who cultured *Oxytricha fallax*, also on *Ps. fluorescens*, and several others. In the last two investigations just referred to the workers suspended the bacteria in a non-nutritive salt solution which resulted in a better quantitative control of the food.

It is not possible here to refer to all of

Leslie (1940a and b) has reviewed the work done in this connection on *Paramecium*. Table 2 shows that the same bacterium has been reported as both suitable and unsuitable as food for this ciliate in a number of instances.

This recent study of Leslie is the most extended study of its kind up to the present. Using over thirty different species of bacteria, carefully standardized as to age and amount used, he tested their suitability as food for *Paramecium multimicro-nucleata*. The tests in most of the cases

were conducted for 30 days. Table 3 shows the results.

The list of bacteria investigated is not extensive enough to permit any generalizations about the suitability of large groups

same species may vary in its suitability as food depending on the age of the culture used. Thus, *Pseudomonas fluorescens* was absolutely unsuitable when taken from 1-day-old cultures but was one of the best

TABLE 3¹
Different bacteria as food for Paramecium

CAT NO.	BACTERIUM	TOTAL PROGENY	DAYS	AVER. NO.	DIV. RATE	SUITABILITY
D-2	<i>Bacillus mycoides</i>	832	27	30	0.5	poor
D-10	<i>Bacillus cereus</i>	1303	29	44	1.1	good
D-20	<i>Bacillus megatherium</i>	1967	29	67	1.6	good
D-21	<i>Bacillus mesentericus</i>	894	27	33	0.6	poor
D-28	<i>Bacillus niger</i>	1086	29	36	0.8	poor
D-41	<i>Bacillus terminalis</i>	942	27	34	0.7	poor
D-39	<i>Bacillus subtilis</i>	655	15	43	1.0	good
D-40	<i>Bacillus subtilis</i>	322	14	23	0.1	poor
K-11	<i>Escherichia coli</i>	1034	29	35	0.7	poor
K-12	<i>Escherichia coli</i>	774	30	25	0.2	poor
A-5	<i>Aerobacter cloacae</i>	1711	29	59	1.4	good
A-6	<i>Aerobacter aerogenes</i>	1372	29	47	1.1	good
Al-2	<i>Erwinia carotovora</i>	1508	29	51	1.2	good
C-1	<i>Alcaligenes fecalis</i>	1670	29	57	1.4	good
T-6	<i>Proteus vulgaris</i>	1224	27	45	1.1	good
Z-1	<i>Serratia marcescens</i>	1260	27	46	1.1	good
AA-2	<i>Spirilla serpens</i>	1077	30	35	0.7	poor
Ad-13	<i>Staphylococcus albus</i>	597	30	19	0.0	poor
Al-1	<i>Erwinia atroseptica</i>	789	30	26	0.3	poor
Am-1	<i>Phytomonas savastanoi</i>	569	30	18	0.0	poor
AM-3	<i>Phytomonas tumefaciens</i>	1910	30	63	1.6	good
AO-1	<i>Cellulomonas blaxtea</i>	618	30	20	0.0	poor
F-1	<i>Actinobacillus lignieresii</i>	645	30	21	0.0	poor
G-17	<i>Corynebacterium ovis</i>	702	30	23	0.1	poor
N-1	<i>Micrococcus luteus</i>	547	30	18	0.0	poor
N-2	<i>Micrococcus ureae</i>	731	30	24	0.2	poor
O-6	<i>Mycobacterium phlei</i>	779	30	25	0.2	poor
O-15	<i>Mycobacterium smegmatis</i>	803	30	26	0.3	poor
O-21	<i>Mycobacterium berolinensis</i>	752	30	25	0.2	poor
U	<i>Pseudomonas ovalis</i>	2117	30	70	1.7	good
*U-6 (5 lines)	<i>Pseudomonas fluorescens</i>	1043	43	24	0.2	poor
*U-6 (5 lines)	<i>Pseudomonas fluorescens</i>	2462	41	60	1.5	good

¹ From Leslie, 1940b.

* 24-hour old bacterium.

4-day old bacterium.

of bacteria as food for *Paramecium*. The result obtained by other workers is shown here, namely, that different strains of the same species may produce different results, e.g., the two strains of *B. subtilis*. Of particular interest here is the finding that the

sources of food when taken from 4- to 30-day-old cultures. This lead, if followed, might result in the finding that many species of bacteria previously designated as unsuitable food organisms, are, under certain conditions, suitable food organisms.

Investigations like those referred to above, while they do not give a real understanding of the nutrition of the protozoans involved in a chemical sense, are important because they have led to a much better control of the food factor in experimental protozoan work than was heretofore practiced.

A few workers have reported successful growth of ciliates in media containing dead microorganisms. Oehler (1919) reported growth of *Colpoda steinii* on dead bacteria and yeast; E. and M. Chatton (1923) cultured *Glaucoma scintillans* on dead bacteria; and Johnson (1936) was able to grow *Glaucoma ficaria* on dead bacteria, dead yeast and dead flagellates. Numerous other workers have not been successful. Luck, Sheets and Thomas (1931) used bacteria killed by a variety of chemical and physical means but could not obtain growth of *Euplotes taylori*. Phelps (1934), using similar methods, failed in attempts to culture *Paramecium aurelia*. Hetherington (1934) found that heat-killed bacteria would not support growth of *Colpidium colpoda*.

In the work on the use of dead bacteria an interesting situation is found. In certain instances the use of dead bacteria of a given species is unsatisfactory as food for a protozoan while the same bacterium in the living state is quite satisfactory as a source of food. E. and M. Chatton found that growth of *Glaucoma* would occur only after the culture media had previously been acted upon by the bacteria used. In other words, if the bacteria were removed from their medium and transferred with the *Glaucoma* to a new medium, no growth of the ciliates took place. This would seem to indicate that the dissolved products of the activity of the bacteria have an important effect on the growth of this form. Glaser and Coria (1935) obtained sterile cultures of two species of *Paramecium* in

media containing either dead yeast or dead bacteria, and, in addition, liver extract and pieces of sterile rabbit kidney. Without the liver extract and the kidney their paramecia would not grow. Leslie (1939) tried dead bacteria as a source of food for *Paramecium* without success. However, in his work he obtained as good growth using bacteria from 30-day-old cultures as he did from 4-day-old cultures. In the 30-day-old cultures, 95 per cent of the bacteria were dead. When he used suspensions of bacteria from young cultures containing one-twentieth the original amount, reproduction was reduced by two-thirds. This would seem to indicate that the presence of a small amount of living bacteria permits the utilization of dead bacteria as food. On the basis of this Leslie has postulated that living *Pseudo-fluorescens* possesses "some growth-promoting substance or food factor for *Paramecium*, the lack of which in suspensions of dead *Ps. fluorescens* may account for its unsuitability."

What, then, is known about growth factors in the nutrition of Protozoa?

Lwoff (1938) has defined a growth factor for a given organism as a substance which that organism is incapable of synthesizing and in the absence of which the organism cannot multiply. Excluded from consideration are the elements, the energy-producing carbon-containing foods, and growth stimulants which the organism can produce itself.

M. Lwoff (1931) has shown that certain blood parasites, Trypanosomes, may be grown in peptone media if hematine is supplied. The hematine is a growth factor. It has been shown that the ciliate *Glaucoma piriformis* and three species of Trypanosomes require Vitamin B₁ for growth (A. and M. Lwoff, 1937, and M. Lwoff, 1937). Elliott (1939) demonstrated that the intact molecule of Vitamin

B₁ is required for growth of the ciliate *Colpidium striatum*. Vitamin B₁ is present in adequate amounts in the peptone medium. He destroyed the Vitamin B complex from the basic medium by adjusting the pH to 9.6 and then heating in the autoclave for 1 hour at 20 pounds pressure. Such treated medium would not support growth past the first transfer; but this treated medium, when crystalline thiamin chloride was added to it, supported excellent growth. Elliott further found that crystalline riboflavin and Vitamin B₆ (concentrate) could not supplant thiamin in the nutrition of *Colpidium*.

Hall and some of his students have shown that none of the ciliates which they have grown in pure culture will maintain growth in a gelatin-dextrose medium, where the only source of nitrogen is the gelatin. However, in 1938 Hall reported that when he added pimelic acid to this medium he was able to carry *Colpidium campylum* through six transfers with good growth. He says, "It thus appears that the failure of the ciliates to grow in gelatin is not dependent necessarily upon the amino-acid deficiencies of the gelatin. The implication is either that the missing amino acids are not essential to life of the ciliates or else that synthesis is possible in the presence of pimelic acid." This acid has been reported as a growth factor for the diphtheria bacillus by Mueller (1937). Cailleau (1938a and b) has found that the two flagellates, *Trichomonas foetus* and *Eutrichomastix colubrorum*, will not grow in the absence of ascorbic acid. Cailleau also found that cholesterol is indispensable for these same two flagellates and for one other, *Trichomonas columboe*. She states that when an alcoholic solution of cholesterol is added to the peptone medium it is precipitated in very fine particles and that the flagellates ingest and utilize these particles.

Lwoff (1932) in discussing the evolution of microorganisms points out that along with the morphological evolution there has been a physiological evolution involving a successive loss of functions as regards their abilities to utilize different compounds as nutrients. The following table (Table 4) illustrates this point.

Thus it is seen that the simplest forms can synthesize their proteins with nitrates as the only source of nitrogen, the next group requires ammonium salts, the next amino acids, the next peptones and finally

TABLE 4*

Loss of functions in evolution of microorganisms

	NITRATES	AMMONIUM SALTS	AMINO ACIDS	PEPTONES	PEPTONES AND AC-TIVE SUBSTANCE
<i>Aspergillus</i>	+	+	+	+	+
Yeasts, <i>Polytoma</i>	o	+	+	+	+
<i>Chlamydomonas</i> and <i>Haematococcus</i> (in the dark)	o	o	+	+	+
<i>Glaucoma piiformis</i>	o	o	o	+	+
Parasitic bacteria and flagellates	o	o	o	o	+

+ organism can utilize.

o organism cannot utilize.

* From Lwoff, 1932.

the parasitic forms are dependent upon some special substance in addition to the peptones.

Lwoff (1938) points out that this same idea—a loss of functions—applies with reference to growth factors. This has been shown for bacteria and it is indicated for protozoans in the next table (Table 5), with reference to Vitamin B₁.

Generally speaking, the first forms in the above table are able to synthesize both parts of the Vitamin B₁ molecule, the next group cannot synthesize the parts but can fuse them if they are furnished and finally *Glaucoma* and the Trypanosomes must be

furnished with the intact molecule of the vitamin. In discussing this, Lwoff points out that a veritable state of symbiosis exists in nature between many organisms—one organism producing one part of a necessary substance, another producing the other part of this substance.

In an earlier paragraph reference was made to the differences in results which have been obtained by various workers in their attempts to grow ciliates in sterile

field of growth factors in protozoans has only been scratched.

It seems worth while, at this point, to go back to Lwoff's original statements about the nature of the nutrition of *Glaucoma* in peptone media. He concluded that this ciliate absorbs substances as complex as peptids and even peptones directly from the medium and that the substances taken into the protoplasm through the surface must be comparable to the substances which enter the protoplasm from the food vacuoles as end-products of digestion when it feeds on particulate food. On this basis, isn't it a reasonable working hypothesis to assume that still other ciliates than those mentioned here may be successfully cultured on media of known compositions? That is, does it not seem plausible that substances comparable to end-products of digestion which can be utilized by other forms may be found, which, along with whatever growth substances may be necessary in each case, in a liquid medium may support growth of other normally holozoic forms?

Frisch (1937) has suggested that the pellicle of *Paramecium* is impermeable to water and salts and probably to gases. If this is true for *Paramecium* and other forms, and if the pellicle forms a barrier to the entrance of dissolved food materials, it still seems that the problem of their nutrition might be attacked by obtaining a properly constituted liquid medium to which is added a finely divided inert substance to facilitate the formation of vacuoles. That ciliates form vacuoles in suspensions of various materials is a common experience. It seems, then, too early in the studies of protozoan nutrition to conclude that a real understanding of the nutritive requirements of the large number of holozoic forms not successfully cultured on media of known composition up to the present will not be obtained.

TABLE 5*
Ability to synthesize vitamin B₁

ORGANISMS	PYRIMIDINE		THIAZOL		VITAMIN B ₁	
	Need	Synthesis	Need	Synthesis	Need	Synthesis
<i>Polytoma obtusum</i> . . .	o	+	o	+	o	+
<i>Polytoma uvella</i> . . .	o	+	o	+	o	+
<i>Polytoma ocellatum</i> . . .	o	+	+	o	o	+
<i>Polytoma caeca</i>	+	o	+	o	o	+
<i>Chilomonas paramecium</i>	+	o	+	o	o	+
<i>Acanthamoeba castellanii</i>	+	o	?	?	o	+
<i>Glaucoma piriformis</i> . .	o	o	o	o	+	o
<i>Strigomonas oneopelti</i> .	o	o	o	o	+	o
<i>Strigomonas culicidarum</i>	o	o	o	o	+	o
<i>Strigomonas fasciculata</i>	o	o	o	o	+	o

* From Lwoff, 1938.

culture on dead bacteria. A few have claimed success; several others have failed. In some quarters doubts have been raised as to whether those workers who claimed success with dead bacteria actually had sterile cultures, free from all living bacteria. Is it not possible, on the basis of the above-mentioned facts, to assume that some ciliates have the ability to synthesize all their needs from dead bacteria, while others may require something furnished by living bacteria? It seems reasonable to suggest that this attitude should be taken in future work. Certainly the

Growth factors, by definition, are substances which an organism cannot synthesize. Substances formed by an organism which accelerate or stimulate growth are in another category. Although not forming a part of the basic nutrient requirements of an organism, such substances are related to the problems of nutrition and growth. As the production of growth stimulating substances has been described in a few species of protozoans in recent years, this matter is considered here briefly.

In 1921 T. B. Robertson reported that when he introduced two Infusoria (either *Enchelys farcimen* or *Colpoda cucullus*) into a small amount of fresh culture medium, the early rate of reproduction was more than double that of a single individual of the same species in the same volume of culture medium. Robertson designated this increased rate of reproduction as the "allelodynamic effect." He postulated that a substance elaborated in the nucleus and given off into the medium at the time of cell division was the cause of this effect.

Numerous investigators, working with a variety of organisms, have tried to repeat Robertson's results, but without success. Johnson (1933), following leads from Chejfec (1929), who cultured *Paramecium* on different concentrations of *B. coli*, and Barker and Taylor (1931) who had observed the effects of different concentrations of *Ps. fluorescens* on the growth of *Colpoda*, was able to obtain results resembling those of Robertson by growing *Oxytricha fallax* in supra-optimal densities of *Ps. fluorescens*. These results were confirmed by Gause (1934), who worked with *Paramecium*. Such results, due to the effects of bacterial crowding, do not fit in with Robertson's postulate of the production of a growth stimulant. Phelps (1935), in studies on *Glaucoma* in pure cul-

ture, reported that he was unable to obtain any indication of the Robertson effect.

The status of this question remained unchanged until recently. Reich (1938) reported results from work on the amoeba, *Mayorella*, grown in bacteria-free cultures on peptone medium, which suggest the production of a growth stimulant by that form. Mast and Pace (1938) state that the colorless flagellate, *Chilomonas*, grown in an ammonium-acetate medium, produces a growth stimulant which soon accumulates in a culture and becomes a growth inhibitor. According to these workers their cultures were sterile. They have demonstrated that this substance is heat-labile. Quite recently (Mast and Pace, 1939) they have reported that this growth stimulating substance will pass through a cellophane membrane with a pore diameter of approximately 6 μ ; and, they suggest that the diameter of the molecules of this substance is slightly less than 6 μ .

Kidder (1939), in a brief note, reports some results with cultures of *Colpidium campylum* grown in bacteria-free peptone-dextrose medium, in the explanation of which he postulates the formation of two substances, one a growth inhibitor which will pass through an asbestor filter and the other a growth accelerator which is absorbed on the filter.

The question of the production of growth stimulants by protozoans is still with us. Additional work is necessary before anything further can be said on the subject.

If this brief review is in a general way a fair statement of the status of our knowledge of protozoan nutrition at the present time, it is obvious that workers in this field still have many interesting and worthwhile problems to solve in future work.

LIST OF LITERATURE

- BARKER, H. A., and TAYLOR, C. V. 1931. A study of the conditions of encystment of *Colpoda cucullus*. *Physiol. Zool.*, 4: 620-34.
- BOND, R. M. 1933. A contribution to the study of the natural food cycle in aquatic environments. *Bull. Bingham Oceanogr. Coll.* Vol. 4, Art. 4, 89 pp.
- v. BRAND, TH. 1935. Der Stoffwechsel der Protozoen. *Ergebn. d. Biol.*, 12: 161-220.
- BUTTERFIELD, C. T. 1929. III. A note on the relation between food concentration in liquid media and growth. *Pub. Health Reports.* 44: 2865-72.
- CAILLEAU, R. 1938a. Le cholestérol et l'acide ascorbique, facteurs de croissance pour le Flagellé tétramitide *Trichomonas foetus* Riedmüller. *C. R. Soc. Biol.*, 127: 861-63.
- . 1938b. L'acide ascorbique et le cholestérol, facteurs de croissance pour le Flagellé *Eutrichomastix colubriformis*. *Ibid.*, 1421-23.
- CHATTON, E., and M. 1923. L'influence des facteurs bactériens sur la nutrition, la multiplication et la sexualité des Infusoires. *C. R. Acad. Sci.*, 176: 1262-64.
- CHEJFEC, M. 1929. Die Lebensdauer von *Paramecium caudatum* in Abhängigkeit von der Nahrungsmenge. *Acta Biol. Experimentalis*, 4: 73-118.
- DUBI, H. 1933. Recherches sur la nutrition de quelques Euglénés. II. *Euglena stellata*, *klebsii*, *anabena*, *deses* et *pisciformis*. *Ann. Inst. Pasteur*, 50: 840-90.
- ELLIOTT, A. M. 1933. Isolation of *Colpidium striatum* Stokes in bacteria-free cultures and the relation of growth to pH of the medium. *Biol. Bull.*, 65: 45-56.
- . 1935. Effects of certain organic acids and protein derivatives on the growth of *Colpidium*. *Arch. f. Protistenk.*, 84: 472-94.
- . 1939. The vitamin B complex and the growth of *Colpidium striatum*. *Physiol. Zool.*, 12: 363-73.
- EPSTEIN, H. 1920. Infektion des Nervensystems von Fischen durch Infusorien. *Arch. Russes. Protistol.*, 5: 177.
- FRISCH, J. A. 1937. The rate of pulsation and the function of the contractile vacuole in *Paramecium multimicronucleatum*. *Arch. f. Protistenk.*, 90: 123-61.
- GAUBE, G. F. 1934. The Struggle for Existence. *Baltimore* (The Williams & Wilkins Co.), 163 pp.
- GLASER, R. W., and CORIA, N. A. 1930. Methods for the pure culture of certain Protozoa. *Jour. Exp. Med.*, 51: 787-806.
- , and —. 1935. The culture and reactions of purified protozoa. *Am. Jour. Hyg.*, 21: 111-21.
- HALL, R. P. 1938. Fimelic acid as a growth factor for the ciliate *Colpidium campylum*. *Anat. Rec.*, 72 (Suppl.): 110 (abstract).
- . 1939. The trophic nature of the plant-like flagellates. *QUART. REV. BIOL.*, 14: 1-12.
- , and ELLIOTT, A. M. 1935. Growth of *Colpidium* in relation to certain incomplete proteins and amino acids. *Arch. f. Protistenk.*, 85: 443-50.
- HARGITT, G. T., and FRAY, W. W. 1917. The growth of *Paramecium* in pure cultures of bacteria. *J. Exp. Zool.*, 22: 24-55.
- HETHERINGTON, A. 1933. The culture of some holotrichous ciliates. *Arch. f. Protistenk.*, 80: 255-80.
- . 1934. The rôle of bacteria in the growth of *Colpidium colpoda*. *Physiol. Zool.*, 7: 618-41.
- JENNINGS, H. S. 1908. Heredity, variation and evolution in Protozoa. III. *Proc. Amer. Phil. Soc.*, 47: 393-546.
- JOHNSON, D. F. 1935. Isolation of *Glaucocystis* Kahl in bacteria-free cultures, and growth in relation to pH of the medium. *Arch. f. Protistenk.*, 86: 261-77.
- . 1936. Growth of *Glaucocystis* Kahl in cultures with single species of other microorganisms. *Ibid.*, 86: 359-78.
- JOHNSON, W. H. 1933. Effects of population density on the rate or reproduction in *Oxytricha*. *Physiol. Zool.*, 6: 22-54.
- . 1937. Experimental populations of microscopic organisms. *Am. Nat.*, 71: 5-20.
- KIDDER, G. W. 1939. The effect of biologically conditioned medium upon the growth of *Colpidium campylum*. *Biol. Bull.*, 78: 297-98.
- LEPEL, J. 1926. Die Infusorien des Süßwassers und Meeres. *Berlin* (Hugo Bermühler), 100 pp.
- LESLIE, L. D. 1940a. Nutritional studies in *Paramecium*. I. Quantitative and qualitative standardization of the food organism. *Physiol. Zool.*, 13: 243-250.
- . 1940b. Nutritional studies in *Paramecium*. II. Bacterial foods. *Physiol. Zool.*, 13: 430-438.
- LOEFLER, J. B. 1934. Bacteria-free culture of *Paramecium*. *Science*, 80: 206-07.
- . 1938. Utilization of dextrose by *Colpidium*, *Glaucocystis*, *Chlamydomonas* and *Chlorogonium* in bacteria-free cultures. *J. Exp. Zool.*, 79: 167-83.
- LUCK, J. M., SHEETS, GRACE, and THOMAS, J. O. 1931. Rôle of bacteria in the nutrition of the Protozoa. *Quart. Rev. Biol.*, 6: 46-58.
- LWOFF, A. 1923. Sur la nutrition des Infusoires. *C. R. Acad. Sci.*, 176: 928-30.

- . 1925. Sur la nutrition des Infusoires aux dépens des substances dissoutes. *C. R. Soc. Biol.*, 93: 1272-73.
- . 1932. Recherches biochimiques sur la Nutrition des Protozoaires. Le Pouvoir synthèse. Paris (Masson et Cie.) 158 pp.
- . 1938. Les facteurs de croissance pour les microorganismes. *Ann. Inst. Pasteur*, 61: 580-617.
- , and DUBI, H. 1938. Culture de divers Flagellés leucophytes en milieu synthétique. *C. R. Soc. Biol.*, 127: 53-56.
- , and M. 1937. L'aneurine, facteur de croissance pour le Cilié *Glaucoma piriiformis*. *Ibid.*, 126: 644-46.
- LWOFF, M. 1931. La nature de la substance du sang indispensable aux Trypanosomides. *Ibid.*, 107: 1234-36.
- . 1937. L'aneurine, facteur de croissance pour le Flagellé trypanosomide *Strigomonas oncopelti*. *Ibid.*, 126: 771-73.
- MAINX, F. 1928. Beiträge zur Morphologie und Physiologie der Eugleninen. II. Untersuchungen über die Ernährungs- und Reizphysiologie. *Arch. f. Protistenk.*, 60: 355-414.
- MAST, S. O., and PAGE, D. M. 1938. The relation between the age of the cultures from which *Chilomonas* is taken and the rate of reproduction in fresh culture fluid. *Anat. Rec.*, 72 (Suppl.): 62 (abstract).
- , and —. 1939. The size of the molecules in the growth substance produced by *Chilomonas paramecium*. *Ibid.*, 75 (Suppl.): 77-78 (abstract).
- MAUPAS, E. 1888. Recherches expérimentales sur la multiplication des Infusoires Ciliés. *Arch. de Zool. Exp. et Gen.*, T. 6.
- MUELLER, J. H. 1937. Pimelic acid as a growth accessory for the diphtheria bacillus. *Jour. Biol. Chem.*, 119: 121-31.
- ORHLER, R. 1919. Flagellaten- und Ciliatenzucht auf reinem Boden. *Arch. f. Protistenk.*, 40: 16-26.
- PETERS, R. A. 1921. The substances needed for the growth of a pure culture of *Colpidium colpoda*. *Jour. Physiol.*, 55: 1-32.
- . 1929. Observation upon the oxygen consumption of *Colpidium colpoda*. *Ibid.*, 68: 11-111.
- PHELPS, A. 1934. Studies on the nutrition of *Paramecium*. *Arch. f. Protistenk.*, 82: 134-63.
- . 1935. Growth of Protozoa in pure culture. I. Effect upon the growth curve of the age of the inoculum and of the amount of the inoculum. *J. Exp. Zool.*, 70: 109-130.
- PHILLIPS, RUTH L. 1922. The growth of *Paramecium* in infusions of known bacterial content. *Ibid.*, 36: 135-83.
- PRINGSHEIM, E. G. 1921. Zur Physiologie saprophytischer Flagellaten (*Polytoma*, *Astasia* und *Chilomonas*). *Beitr. allg. Bot.*, 2: 88-138.
- REICH, K. 1935. The cultivation of a sterile amoeba on media without solid food. *J. Exp. Zool.*, 69: 497-500.
- . 1938. Studies on the physiology of amoeba. The allelocatalytic effect in amoeba cultures free of bacteria. *Physiol. Zool.*, 11: 347-58.
- ROBERTSON, T. B. 1921. Experimental studies on cellular multiplication. I. The multiplication of isolated Infusoria. *Biochem. Jour.*, 25: 595-611.
- SANDON, H. 1932. The Food of Protozoa. Cairo (Misr-Sokkar Press), 187 pp.





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BRIEF NOTICES

EVOLUTION

GEOLOGY OF THE CLEVELAND REGION. *Pocket Natural History* No. 9. *Geological Series* No. 1.

By Arthur B. Williams. *Cleveland Museum of Natural History, Cleveland, Ohio.* 50 cents. 6½ x 4½; 61; 1940 (paper).

Although this little handbook was prepared especially for use in the Cleveland region, it also contains brief and interesting discussions on topics of general interest, such as geologic time, ancient American inland seas, culture as related to geology, and the influence of glaciation upon present distribution of human populations.

Within the state of Ohio there are two distinct physiographic areas: (1) the southeastern, unglaciated plateau of a rugged contour; and (2) the northeastern and western section of glaciated, smooth plateau land. The boundary between these two regions is roughly marked by the Portage Escarpment, a bold and steep rise from the glaciated area to the unglaciated section which corresponds generally with the southernmost extent of the glaciers of the great ice age of 20,000 years ago. Appended to the text are a short glossary and a list of bibliographic references.



GENETICS

FARM ANIMALS: *Their Breeding, Growth, and Inheritance.*

By John Hammond. *Longmans, Green and Company, New York; Edward Arnold and Company, London.* \$4.50. 8½ x 5½; viii + 199; 1940.

The ever increasing importance of agricultural products in our present world economy has been responsible for the effort, on the part of specialists in plant and animal husbandry, for continual improvement in their various fields. The successes, failures, and most promising lines for future work in the breeding and rearing of farm animals are neatly pointed out in this volume.

Part I of the text deals specifically with the physiology of sex, reproduction and growth of the five standard farm animals: i.e. horses, cattle, sheep, pigs, and poultry. The discussion of the sex of these animals as related to nutrition, endocrine activity, and general body health, constitutes an introduction to the more detailed accounts of the breeding season, the oestrus cycle, fecundity and fertility, viability of sperm and ova, sterility, artificial insemination, pregnancy, gestation, and parturition in the several forms. The problem of growth and development has been presented from the point of view of differential gradients in relation to nutrition and to the type of body build desired; the importance of this knowledge to both the farmer and the butcher is emphasized.

Part II discusses the relationship between genetics and modern methods and practice in animal breeding. Though a superior genetic make-up is admittedly

essential for the production of superior animals, the importance of selection and nutrition is not minimized.

The text is well illustrated, documented and indexed. It is an authoritative work that will find favor not only with the animal breeder, but with the general farmer whose breeding of animals is necessarily limited.



ELEMENTS OF GENETICS. *Mendel's Laws of Heredity with Special Application to Man.*

By Edward C. Colin. The Blakiston Company, Philadelphia. \$3.00. 8 $\frac{3}{8}$ x 5 $\frac{1}{2}$; xii + 386; 1941.

It has been the aim of the author to make this book interesting by weaving material on human genetics throughout the pages of an elementary text. In large measure the attempt has been successful. The simplest and accepted mechanisms of human heredity are presented in the early chapters, while those which are less well established are left to a separate section dealing largely with the inheritance of diseases.

In its scope the volume covers the same material as other elementary texts, but it contains little information on the statistical methods of measuring variations, which is an important factor, especially in the study of human inheritance. In placing his emphasis on man, Colin has neglected to show the widespread application of genetics to domesticated animals and plants. Although sparsely illustrated the book contains a glossary and a thorough index.



GENERAL BIOLOGY

PHYTOPLANKTON AND PLANKTONIC PROTOZOA OF THE OFFSHORE WATERS, GULF OF MAINE. *Transactions of the American Philosophical Society Held at Philadelphia for Promoting Useful Knowledge. New Series, Volume XXXI, Part III.*

By Henry B. Bigelow, Lois C. Lillick and

Mary Sears. *American Philosophical Society, Philadelphia.* \$1.75. 12 x 9 $\frac{1}{4}$; 91; 1940 (paper).

Collections of plankton made from the "Atlantis" at representative localities in the Gulf of Maine at various times of the year in 1933 and 1934 and in August, 1936, furnished the material for the two parts of this report. In the first—Numerical Distribution, by the three authors mentioned in the heading—planktonic protozoa were demonstrated to be at their numerical minimum from mid-autumn through the winter, with the regional variation wider in January than in any other month, with the most abundant winter population (900,000–1,000,000 per column) in shoal water close to Cape Cod and on the eastern part of George's Bank. Midsummer was marked as the season for maximum number of protozoa (about 4,000,000 per column).

The next to the smallest count for protozoa (11,000 per column) was only about 1/8 as great as the smallest for phytoplankton; the largest for protozoa (10,700,000) about 1/1295 as great as the largest for phytoplankton; the grand average for protozoa only about 1/337 that for phytoplankton. These contrasts sufficiently emphasize the paucity of the waters of the Gulf of Maine in unicellular animals as contrasted with unicellular plants.

The results of the second part—Qualitative Composition of the Planktonic Flora, by Lois C. Lillick—show that:

The scanty winter flora of the Gulf of Maine (usually dominated by *Coscinodiscus*, by *Ceratium*, or by other small peridinians) is succeeded by the vernal outbursts of diatoms and a decrease in the abundance of peridinians. This flowering results chiefly from the rapid multiplication of *Thalassiosira*. . . . The area of the *Thalassiosira* flowering expands northward along shore on both sides of the gulf, also southward and offshore into the eastern basin and to a certain extent into the western basin and over the eastern part of George's Bank. Active multiplication is briefest (2–4 weeks) in the eastern and southeastern parts of the gulf generally, longest in the northern coastal belt. After reaching its peak, *Thalassiosira* falls within a few days to an insignificant rank in the flora.

Accompanying the eclipse of *Thalassiosira*, there is a flowering of *Chaetoceros*, which lasts from 4–6 weeks over the gulf generally (i.e., until late April–May). Once its peak of abundance is passed, *Chaetoceros* declines as abruptly in abundance as *Thalassiosira*.

Both papers are illustrated with maps,

the second also with diagrams, and each paper has its own bibliography.



WILDLIFE CONSERVATION.

By Ira N. Gabrielson. *The Macmillan Company, New York.* \$3.50. 9½ x 6; xv + 250; 1941.

In this book the Director of the Division of Fish and Wildlife has written an authoritative treatise on the problems of conservation and the best means of meeting them. Conservation has been beset with continued bickerings and prejudices; the hunters and trappers, the nature lovers, the timber interests, the farmers, are but some of the many who have raised objections to whatever policy was pursued. Selfish motives, and more especially, a lack of appreciation and comprehension of what conservation consists of and what it aims to do, are in part responsible for a lack of mutual understanding. This book furnishes a broad foundation for a proper evaluation of conservation, stressing particularly the interrelations of soil, water, forest, and wildlife to the problem as a whole. The more detailed and analytical phases of conservation as exemplified by recent studies have been omitted—a wise procedure in view of the fact that this science is complex enough without introducing technicalities that would obscure the basic background that the author desires to establish.

The book fills an obvious gap. It is recommended that all those interested in our natural resources read it, especially those who have set ideas on the subject without really knowing why. Many photographs from the departmental files are used as illustrations. Unfortunately there is no bibliography.



PAPERS FROM TORTUGAS LABORATORY. Volume XXXII. *Carnegie Institution of Washington Publication No. 517.*

Carnegie Institution of Washington, D. C. \$4.50 (cloth); \$4.00 (paper). 10 x 6½; iv + 412 + 12 plates; 1940.

The papers from the Tortugas Laboratory have long been noted as significant contributions in the general field of marine biology. The present volume contains sixteen papers (by nineteen investigators) which deal with a variety of subjects, such as larval metamorphosis of the ascidian; the structure, composition, and growth of *Valonia*, and its reaction to light; the photosensitivity of *Crangon* and *Panulirus*; the chromatophore system and chromatophore reaction of *Crangon* and *Pomacentrus*; the structure of zooxanthellae and their symbiotic relation to *Tridachia*; and the ecology and geology of the Florida mangroves.

Of particular interest and significance is the long and detailed paper by Longley (late executive officer of the Tortugas Laboratory) and Hildebrand, in which the junior author, with the aid of Longley's notes and unpublished data, describes two new genera and fifteen new species of fishes common to the Tortugas. In a paper by Bullington, one new genus and nine new species of marine ciliates are described.

Each paper in the volume is provided with a short table of contents and a bibliography.



CARNEGIE INSTITUTION OF WASHINGTON YEAR BOOK No. 39, July 1, 1939–June 30, 1940. *With Administrative Reports through December 13, 1940.*

Carnegie Institution of Washington, D. C. \$1.50 (cloth); \$1.00 (paper). 10 x 6½; xxxi + 326; 1940.

In the present issue of the Carnegie Year Book, fully half of the volume (171 pages) is devoted to biological and allied subjects. It is of interest to have at hand this summary dealing with the progress of the work throughout the year and the future lines of research in the different departments. The various monographs are seen by many as they are issued but no adequate conception of the detailed program of study can be obtained except through the Year Book. Following the reports of the Division of Plant Biology, the Department of Embryology, the Department of

Genetics, the Nutrition Laboratory and the Division of Historical Research there are reports on Special Projects in these various fields. The volume concludes with a list of publications issued by the Carnegie Institution during 1939-40 and a detailed index.



BIOLOGY

By Howard M. Parsbley. *John Wiley and Sons, New York; Chapman and Hall, London.* \$2.25. 8½ x 5½; ix + 232; 1940.

This book is a brief survey of the main facts and principles of modern biology. Its aim is to present the knowledge in this field which seems essential to a liberal education and therefore appropriate as the biological portion of a course in general science. A large subject has been brought within narrow limits by an elimination of technical detail which, while rather drastic, is intended to be not inconsistent with scientific accuracy and clarity. The excellent illustrations have been selected with special care. There is a bibliography at the end of each chapter, and, in addition, a complete list of references has been included in the appendix, which contains, in addition, a list of highlights of biological history and a glossary. A complete index concludes the volume. Designed as it is for a college survey course in science, this volume should effectively serve its purpose.



NATURE SMILES IN VERSE. *A Collection of Bi-illlogical Poems.*

Compiled by Bernal R. Weimer. *Illustrations by Bobby Murray.* B. R. Weimer, *Bethany College, Bethany, W. Va.* \$1.50. 9 x 6; x + 99; 1940.

This is an anthology of poems dealing with biological subjects, some of which are quite clever and all of which honestly try to be. Among the former are such old time favorites as Bert Leston Taylor's *The Dinosaur* and Charlotte Perkins Gilman's *Eobippus*, and among the latter numerous effusions that quite obviously

were not intended for publication. The critical reader is likely to miss that delightful verse by Laura E. Richards about the "sculpin that was gulpin' of his tea, deary me," and to wonder why the compiler saw fit to commit mayhem on the masterpiece by Gelett Burgess about the lightning bug and the measuring worm.



HUMAN BIOLOGY

FIRST EXPEDITION OF VARGAS INTO NEW MEXICO, 1692.

Translated, with Introduction and Notes by J. Manuel Espinosa. The University of New Mexico Press, Albuquerque. \$4.00. 10½ x 6½; xi + 319; 1940.

The Spaniards, in enlarging their possessions in the Western World after their conquest of Mexico, pushed far north into what is now New Mexico and Arizona. It had been their expectation that this region, a land of mystery, would be as productive of wealth as were the countries to the south. Coronado, however, returned empty-handed so far as gold and silver were concerned, but he brought marvelous tales of what lay beyond the regions he had traversed. During the seventeenth century the non-aboriginal population of New Mexico never exceeded 3,000. Santa Fe had been established as the capital of the province in 1610. The pueblo Indians, of a peaceful nature, were taught the language of their conquerors and practiced outwardly their religion. The governors of New Mexico, being far from the main seat of authority, failed as the years passed by to carry out Spain's humane Indian laws. Growing discontent among the natives finally resulted, in 1680, in a successful revolt. For twelve years the Indians held New Mexico as their own, in spite of large sums of money spent by the Spaniards in reconquest. By this time it was realized that the real value of New Mexico to the Spanish provinces lay in the fact that this region was a bulwark of defense not only against Indian attacks from the whole northern frontier but also from the French and Indians who were pushing in from the east.

Early in the last decade of the seventeenth century Diego de Vargas was given the task of reconquest. A preliminary expedition in 1692 paved the way for a much larger expedition in 1693, with settlers, missionaries, and live stock. Many pueblos were found willing to accept Spanish rule, while others, fearing punishment for the crimes of 1680, were subdued with difficulty. Victorious campaigns of Vargas in 1694 were followed by increased numbers of settlements and within the next few years New Mexico was laying the foundations of self-sufficiency and permanency. What scattered rebellions occurred Vargas met with a series of swift revengeful campaigns.

In the present volume following the Introduction, which we have so briefly summarized, the documents which deal with the first phase of the reconquest of New Mexico are given in full. These are as follows:

Document I. Report of the finance committee of the government of New Spain, Mexico city, May 28, 1692, officially authorizing Don Diego de Vargas to reconquer New Mexico (5 pp.); Document II. Vargas' campaign journal and correspondence, August 21 to October 16, 1692 (118 pp.); Document III. Vargas' campaign journal correspondence, October 16, 1692, to January 12, 1693 (112 pp.); Document IV. Letter from Don Diego de Vargas to the Conde de Galve, El Paso, January 12, 1693, concerning the settlement of New Mexico (12 pp.); Document V. Report of Conde de Galve to Don Diego de Vargas, Mexico city, November 24, 1692 (7 pp.); Document VI. Report of the general junta, Mexico city, February 25, 1693 (7 pp.); Document VII. Order of the Conde de Galve to Don Diego de Vargas, Mexico city, April 18, 1693 (5 pp.).

We have in this book not only new light on a stirring chapter in the history of the American frontier, but much interesting material on the pueblo Indians. The volume is carefully indexed.



THE MAYA AND THEIR NEIGHBORS. Limited Edition.

By Clarence L. Hay, Ralph L. Linton, Samuel K. Lothrop, Harry L. Shapiro, George C. Vaillant et al. D. Appleton-Century Company, New York and London. \$6.00. 9½ x 6; xxiii + 606; 1940.

It is difficult in a brief space to do justice

to this scholarly book, written by a group of specialists each one of whom is a student of some particular phase of Middle American archaeology. Its purpose is to offer a summary of current opinion in this field which will be "a critical guidance toward an understanding of the basic nature of the subject or toward following the general direction of the research." A vast literature has accumulated concerning Middle American archaeology but it is too formidable a list for the consideration of the student in other lines of work or the serious lay reader who is in search of background reading on Indian civilization.

Within the covers of this book will be found a fine collection of essays, thirty-four in number, grouped under four section headings. In Part I, The Background of the Maya, an analysis of the basic factors underlying the racial affiliations of the American Indian is given, followed by discussions on such subjects as the basic physical factors affecting Middle America, food supplies essential for existence, native languages, and an analysis of the different linguistic maps made for the Middle Area. In Part II, The Maya, the essays deal with the development of Maya civilization in relation to the problems of Middle American culture in general, the latest research in the highest centers of Maya civilization, the history of the decipherment of the Maya inscriptions (a feat of scholarship almost on a par with the formulation of the original graphic system), Maya and Christian chronologies, astronomy, architecture, ceramics, skeletons from the Cenote of Sacrifice at Chichen Itzá and the transformation of the modern Maya from the manner of life of their ancient predecessors. In Part III, The Northern neighbors of the Maya, the discussions are on the basic difference between the Middle American cultures and those of North and South America, the contemporaneity of the advanced civilizations of the Toltec and Zapotec, archaeology and pottery, and Mexican influences upon the Indian cultures of the southwestern United States in the 16th and 17th centuries. Part IV. The Southern neighbors of the Maya, is concerned with the southern limits of Maya civilization, archaeological

remains of Honduras, non-Maya monumental sculpture of Central America, the diffusion of culture from Middle America and the effect on the cultures of South America, and South American penetrations in Middle America. The final essay is a critical synthesis of the essays contributed to the volume in their relationship to American anthropology as a whole.

Accompanying the text are 20 plates, 40 illustrations, a linguistic map of Mexico and Central America, and 11 tables. A bibliography of 103 pages and an index conclude the volume.



THE MAORI PEOPLE TODAY. A General Survey.

Edited by I. L. G. Sutherland. Issued under the Auspices of The New Zealand Institute of International Affairs and The New Zealand Council for Educational Research. Oxford University Press, New York. \$4.00. 8½ x 5½; xiii + 449; 1940.

The New Zealand Institute of International Affairs, an unofficial and non-political body, has for its object the promotion of an understanding of international questions and problems particularly in so far as these may relate to New Zealand, the British Commonwealth, and the countries of the Pacific Area.

The nine authors, who contribute the twelve chapters of the present volume, are all specialists on some phase of Maori life, and one of them, Sir Apirana Nyata, is an outstanding member of the Maori group. They present a study "designed to put on record the present position of the race and to discuss its problems at what appears to be a critical stage in its history."

The Maori people, one of the most interesting of the Polynesian races, made their great migration from the tropical islands of the Eastern Pacific to New Zealand about six centuries ago (circa 1350). Although new modes of living, necessitated by a much colder climate, and variations in their tribal customs, due first to their long isolation from other Polynesians and later to their contacts with European settlers, created many changes in their customs, the background

of their culture is still that of the Polynesians. We are given much that is of interest concerning the main features of the Maori and early European settlers, tribal organizations, economic conditions, education, arts and crafts, and religious influences, with a final summing up of the present Maori situation by Sutherland.

The volume contains a number of illustrations, a glossary, a brief list of references and a detailed index.



NORWEGIAN MIGRATION TO AMERICA. The American Transition.

By Theodore C. Blegen. Norwegian-American Historical Association, Northfield, Minnesota. \$3.50. 8½ x 5½; xii + 655; 1940.

In an earlier monograph Blegen described the Norwegian immigration of the first half of the 19th century and the factors that determined it. In this volume the account is continued and concerns primarily the processes which led to the integration of the Norwegian group with the rest of the population of this country. The author depicts in detail the conditions of the immigrants when they arrived, the culture that they brought with them and their reactions to the culture of their adopted country. The immigration was in general by family groups and the immigrants on the whole appeared as closed colonies which centered around the church. Because of this, the individuality of the Norwegian settlements was retained for some time and until, through the public schools, the offspring of the immigrants gained access to the mores of this country. The most important political event which transformed passive participation in the affairs of the country to an active one was the Civil War. Then, the Norwegians began to identify themselves with the nation that had given them hospitality. In describing the folkways of the immigrants, the development of their schools and of higher education, and their transformation into Americans, the author has had recourse to original sources. Moreover, the style in which the subject is written is far from pedantic so that this work makes for enjoyable reading besides presenting a clear-cut picture

of the pattern of the processes of amalgamation of peoples within our country.



NEW HAVEN NEGROES. *A Social History.*
By Robert A. Warner. Yale University Press, New Haven; Oxford University Press, London. \$3.50. 9 x 5½; xiv + 309; 1940.

It is to be hoped that some day the social relations between Negroes and whites will attain a status satisfactory to both groups. In the meantime thoughtful persons and especially those who sincerely believe in the principles of freedom, cannot help but be distressed by the white man's actions with respect to the Negro. The account presented in this book is not very different from that which can be reported from other communities, except that New Haven is one of the oldest civilized centers of the country so the conduct of its population seems even more unpleasant. In Connecticut the Negroes were emancipated in 1784 but still in 1864 they were little better off than the Negroes elsewhere and had not made appreciable progress toward the achievement of their rights. The author emphasizes two points about the history of the Negro in New Haven. The first is the struggle to be permitted to have formal education. The long fight and the political partisanship involved are tersely described and make for thrilling reading. The second point is the formation of castes. For the Negro today as well as for the whites the circulation of the social classes is being reduced considerably. As in all other communities, so in New Haven the Negro occupies the lowest rank, and for some reason the author believes that this is an indication of progress on the part of the Negro. Although rather narrow in outlook, this monograph is interesting because of its subject and the efforts of the author to make an extensive survey of the situation and its origins.



THE IMMIGRANT IN AMERICAN HISTORY.
By Marcus L. Hansen. Harvard Uni-

versity Press, Cambridge. \$2.50. 8 x 5½; xi + 230; 1940.

This book consists of nine essays on a subject about which the author was one of the foremost specialists. Several of the broad aspects of the immigration to this country form the topics of these essays; first of all being the movement of the first half of the 19th century and all the hardships associated with leaving the country of origin and settling in the new country. The author has made use of contemporary accounts and they are both tragic and amusing. Preoccupations relative to religion were foremost in the minds of the immigrants. The process of adapting religious customs and views to a new environment was one factor responsible for the multiplicity of sects into which some of the denominations split. Hansen sought also to evaluate the contributions of the several national groups to the civilization of this country. He cast a doubtful eye on the pretensions of the descendants of the several foreign groups but was himself unable to arrive at any sound measure of their contributions. Without doubt some time will pass before an adequate and objective determination can be achieved. It cannot be said that new facts are brought out in this volume, but the presentation of the subject will certainly stimulate a clearer understanding of the elements that entered into the formation of our nation.



ON SAFARI.

By Theodore J. Waldeck. With Illustrations by Kurt Wiese. The Viking Press, New York. \$2.50. 8½ x 5½; 208; 1940. *On Safari* is an excellent collection of adventure stories as well as an elucidative text for embryonic explorers. The author, a famous explorer, has selected anecdotes from his many African adventures and the result is a collection of exciting tales of life on the Dark Continent. These stories are also instructive as to what Africa demands in courage, scientific knowledge, skill, and leadership to unravel her many secrets and survive all dangers on safari. Waldeck's first experience, about which he writes most

entertainingly, was at the age of 18 on the Duke of Mecklenburg's expedition in 1912. His second African trip occurred seven years later on an expedition under the leadership of Professor Leo Frobenius to the mysterious city of Makala in Zululand. Later, he organized his own expeditions, the first of those being the Waldeck-Smith Expedition in 1924. One of his most interesting African experiences occurred in Abyssinia with the Gallas, Coptic Christians, who almost killed him and his partner Smith, then cured them when they lay ill of fever, and later entertained the explorers in regal, if rather unhygienic and crude, fashion. Lastly, the author relates the exciting story of his initiation into the Secret Order of Lion Men of the Masai, one of the oldest fraternal organizations in the world. Kurt Wiese executed the excellent illustrations which accompany the text.



BIOLOGIE DER GROSSSTADT. IV. *Frankfurter Konferenz für medizinisch-naturwissenschaftliche Zusammenarbeit am 9. und 10. Mai 1940.*

Edited by B. de Rudder and F. Linke. Mit Unterstützung der Stadt Frankfurt a. M. Theodor Steinkopff, Dresden and Leipzig. RM. 8 (in Germany); RM. 6 (outside of Germany). 9½ x 5½; xi + 210; 1940 (paper).

The papers included here were read at the Fourth Frankfurt Conference for Medical and Scientific Cooperation, held on May 9 and 10, 1940. In the first paper "Anthropology of the City," von Verschuer discusses the probability of a relationship between urbanization and (a) increase in body growth and (b) acceleration in development of city children as compared with those in rural districts; fertility and the birth rate. His conclusion is that the large city is "the grave of racial strength and the cultural endowment of our people." One other paper, by Bennholdt-Thomsen, treats the developmental acceleration of the city child. Other papers are concerned with: the origin and growth of cities (W. Polligkeit); characteristics

of industrial cities (W. Brepohl); animal populations of cities (H. Giersberg); influence of the urban milieu on diseases of children (B. de Rudder); the differences between country and town from the psychiatric viewpoint (K. Kolle); and various offerings on the health, nutrition, and hygiene of the city dweller.

Bibliographic references or notes and illustrations accompany some of the papers. Author and subject indices are provided for the volume.



DEALING WITH DELINQUENCY. *Yearbook National Probation Association 1940.*

Edited by Marjorie Bell. The National Probation Association, 1790 Broadway, New York. \$1.75 (cloth); \$1.25 (paper).

8½ x 5½; 341; 1941.

This volume contains the papers read at the 1940 meeting of the National Probation Association held at Grand Rapids, Michigan. Twenty-two articles are segregated under nine different headings. These include the more important aspects of the problems of treatment and prevention of crime and delinquency, creation of clubs and playgrounds to curb juvenile delinquency, social service work associated with probationary activities, administration of probationary and parole systems, popularization of law enforcement and crime prevention measures. In addition there is included in this issue a digest of current legislation concerning probation and parole systems and juvenile courts, and a statistical and financial statement of the Association's work during 1940. At its inception the National Probation Association resembled in certain respects the church organizations with their holy, if unapproachable, objectives. Such attitude was soon abandoned and as one can see from the present report, the members of the Association view the broader sociological and biological factors in crime and attempt to direct their activities accordingly. If this attitude continues and is further extended the great contributions made by the Association towards

crime prevention will be still more increased.



MAN: The Mechanical Misfit.

By G. H. Estabrooks. *The Macmillan Company*, New York. \$2.50. 8 x 5½; 251; 1941.

As the title indicates, the author of this volume endeavors to prove that man is a mechanical misfit and will sooner or later be as extinct as the dinosaur and the saber-toothed tiger. In support of this argument, it is claimed that the skeleton is deteriorating, the internal organs are inadequate, and, worst of all, the brain and nervous system is a curse to man. Similarly, man by thwarting nature's device of weeding out the unfit, has preserved the unfit and encouraged their reproduction, so that natural selection is becoming less and less effective. The author believes that industrial progress, inventive genius and preventive medicine are really "softeners of the race," rendering it unfit to survive in the raw world of nature if its artificial safeguards should ever be swept away. The solution for all of these problems, says the author, is to sterilize all the unfit for one generation, and thus solve all the hereditary problems at one blow, and at the same time eliminate war. Although many readers may not agree with the author's indictments and conclusions, they cannot help but find them immensely stimulating and provocative. The book is indexed, but has no bibliography.



FAMILY INCOME AND EXPENDITURES: Middle Atlantic, North Central and New England Regions. Part 1, Family Income. U. S. Department of Agriculture Miscellaneous Publication No. 383. *Consumer Purchases Study. Farm Series.*

By Dorothy S. Martin, Day Monroe, Dorothy S. Brady, and Elizabeth Phelps. *Government Printing Office*, Washington, D. C. 25 cents. 9½ x 5½; iv + 258; 1940 (paper).

FAMILY INCOME AND EXPENDITURES: Five Regions. Part 2, Family Expenditures. U. S. Department of Agriculture Miscellaneous Publication No. 396. *Consumer Purchases Study. Urban and Village Series.*

By Dorothy S. Brady, Day Monroe, Elizabeth Phelps, and Edith D. Rainboth. *Government Printing Office*, Washington, D. C. 40 cents. 9½ x 5½; iii + 410; 1940 (paper).

Earlier numbers of both the Farm Series and the Urban and Village Series have been noticed in these columns from time to time as they have appeared. The present parts follow the general pattern and purpose of the earlier numbers, namely to show how families in different sections of the United States, in different types of communities, and in different income and occupational groups spend their money.



ASSAM ADVENTURE.

By F. Kingdon Ward. *Jonathan Cape*, London. 12s. 6d. net. 7½ x 5½; 304 + folding map; 1941.

Captain Ward, accompanied by Tashi and Pemba, two Sherpas from Darjeeling, made an expedition of 1,100 miles from Assam over the Great Himalayan Range into the rugged wilds of Southern Tibet. The story of this journey, made in 1935—much of it over territory previously unexplored—is interestingly told. Superimposed are observations of the flowers, people, and geography of the Balipari Frontier Tract made on a second visit three years later. The book should be of interest to several types of readers. The descriptions of the plant finds will fascinate botanists and gardeners, particularly those interested in rock gardens, for which many of the Tibetan plants are most suitable. There is sufficient adventure to attract the general reader interested in travel books. The observations of the people and their customs will interest the ethnologist, and the descriptions and maps of "new" territory, the geographer. Appendix I gives a summary of the marches and Appendix II a list of Tibetan

plants. There are sixteen photographs showing plants, people, and places.



ACCULTURATION IN SEVEN AMERICAN INDIAN TRIBES.

Edited by Ralph Linton. D. Appleton-Century Company, New York and London.

\$4.00. 8½ x 5½; xiii + 526; 1940.

Herein are presented tribal studies on the acculturation process in seven American Indian tribes, namely: the Puyallup of Washington, the White Knife Shoshoni of Nevada, the Southern Ute of Colorado, the Northern Arapaho of Wyoming, the Fox of Iowa, the Alkatcho Carrier of British Columbia, and the San Ildefonso of New Mexico. The seven reports, presented according to a detailed "Outline for report on acculturation in any given tribe" which appears in the introduction, represent original field work by the author. Many new unpublished ethnological data are given. Linton briefly summarizes each of these studies and in the last three chapters of the text defines acculturation and the culture concept and discusses the processes of culture change, culture transfer, and the distinctive aspects of acculturation. The volume is indexed.



CATTLE, HORSES AND MEN OF THE WESTERN RANGE.

By John H. (Jack) Culley. Illustrations by Katherine Field. The Ward Ritchie Press, Los Angeles. \$3.00. 9 x 6; xvi + 337; 1940.

Here is a truly delightful account of one of the colorful periods of American history—from about 1865 to 1900—which had to do with the development of the range cattle business in the western half of the United States. The author has been one of the actors in the great drama of the west and speaks authentically of the characters and events comprising the life in this romantic period of our history. The first part of the book deals with life on the famous Old Bell Ranch, in New Mexico, of which the author became ranch manager; the second part with horses as Culley

learned to know, understand and train them during his years in the ranch business. In the third part of the volume, the cattle and men who were the major participants in this saga of the west are described in detail. The delightful illustrations are by Katherine Field. The book makes entertaining and instructive reading and has been indexed for the use of scholars.



EVIDENCE OF EARLY INDIAN OCCUPANCY NEAR THE PEAKS OF OTTER, BEDFORD COUNTY, VIRGINIA. *Smithsonian Miscellaneous Collections, Volume 99, Number 15.*

By David I. Bushnell, Jr. Smithsonian Institution, Washington, D. C. 20 cents.

9½ x 6½; 14 + 5 plates; 1940 (paper).

In this brief monograph the author has outlined the evidence pointing to early Indian occupancy in the vicinity of the Peaks of Otter, Bedford County, Virginia. The Mons site, so called because part of the settlement was found on the grounds of the recently demolished resort hotel, Hotel Mons, was exposed during the spring of 1940 during work on the extension of the Skyline Drive. Following a discussion on the region in which the ancient Indian settlement was found, there is a descriptive section, with accompanying plates, on the artifacts, including two Folsom points and pottery fragments, uncovered on the site. There are nine illustrations—five plates and four figures, the latter including a reconnaissance map of Bedford.



SOCIAL AND ECONOMIC ASPECTS OF SWEDISH POPULATION MOVEMENTS 1750-1933.

By Dorothy S. Thomas. Macmillan Company, New York. \$6.00. 8½ x 5; xxiii + 487; 1941.

The Swedish vital and economic statistics are generally regarded as the most complete of any such statistics, and contain the longest continuous series of census data. Much use has been made of these data by several statisticians and the author has sought to bring the series

further to date and to complement the data with other pertinent information. For the years 1750 to 1933 the statistics given concern the population and its movements, agriculture and industry. For a shorter number of years, from 1895 to 1933, the data refer to urban and rural communities into which Sweden is segregated. With minor exceptions the author has limited herself to an exposition of the statistics in a manner not much more discursive than the yearbooks published by governmental agencies. However, credit is due Thomas for making such valuable data easily available to all students.



RASSENKUNDE UND RASSENGESCHICHTE DER MENSCHHEIT. Erster Band. Die Forschung am Menschen. Fünfte Lieferung (Bogen 32-39). Zweite umgearbeitete und erweiterte Auflage.

By Egon Freiherr von Eickstedt. Ferdinand Enke Verlag, Stuttgart. RM. 10. 10½ x 7; 497-624; 1940 (paper).

Numbers 1, 2, 3, 4, 6, and 7 of this second edition have already been noticed in these columns at various times since Volume 3, Number 3. As in these earlier *Lieferungen* the revision and additions in the present number have been extensive. Fully annotated, it treats type analyses and type characters, and begins the discussion on methods of research on the make-up of population groups (studies on twins, number of children in families, paternity tests, pedigrees, statistics on marriage, population, migration, etc.)



THE WARS OF THE IROQUOIS. A Study of Intertribal Trade Relations.

By George T. Hunt. University of Wisconsin Press, Madison, Wisconsin. \$3.00. 9½ x 6; 209; 1940.

The subtitle is the key to the nature of this penetrating study. The author does not treat the Iroquois as aggressors who made war for its own sake. He considers them as a people who were primarily traders,

and who, when faced with the possible loss of their trade, chose to fight to maintain it. In the end they became the dominant tribe in the so-called League of the Iroquois, influential far to the north and south of their territory, and accordingly valuable as allies of the English in the wars with the French in Canada. It is interesting to note that the author does not think the Indians were as well supplied with firearms as is commonly supposed.



VERHANDLUNGEN DER DEUTSCHEN GESELLSCHAFT FÜR RASSENFORSCHUNG. Band X. Vorträge gehalten am 24. und 25. März 1939 auf der 10. Tagung in München. Sonderheft zum XVI. Jahrgang des Anthropologischen Anzeigers.

Edited by B. K. Schultz. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. RM. 16.95. 10 x 6½; xx + 168 + 17 plates; 1940 (paper).

The list of authors of the 24 lectures contained in this volume includes Th. Mollison, J. Schwidetzky, H. Weinert and O. Reche, among others well known in their respective fields. The lectures deal with newer anthropological findings, race history and ethnology, and a few miscellaneous items such as sex differences in the performance of sports. Most of the papers are based on German material.



INDIAN POPULATION PROBLEMS. Report and Proceedings of the 2nd All-India Population and 1st Family Hygiene Conference, 1938.

Edited by G. S. Gburey. Karnatak Publishing House, Bombay. Rs. 5. 9½ x 6½; 332 + xii + [7]; 1940 (paper).

The papers collected in this volume are organized according to the sections before which they were read: Birth control and sterilization; Medical problems and problems of sex; Maternity and child welfare; Housing and health; Vital statistics; Economics; Sociology; and Nutrition. Some abstracts of papers received but not read at the meetings are included at the ends of the proper sections. Most of the

material is based on studies made in India.



BORN THAT WAY.

By Earl R. Carlson. *The John Day Company, New York.* \$1.75. 7 $\frac{1}{8}$ x 5; ix + 174; 1941.

This is an autobiography written to offer encouragement to the physically handicapped. Such a person who reaches the goal he has chosen merits praise from all of us. When that person then uses the knowledge he has gained in his own struggle for success to help others crippled as he is, we feel that his success is well deserved. Its very nature makes this a personal story, but it is not sentimental; rather, it is an account of a life-long campaign which requires a great deal of energy and will power.



ZOOLOGY

INSECT PESTS.

By W. Clunie Harvey and Harry Hill. H. K. Lewis and Company, London. 10s. 6d. net. 7 $\frac{1}{4}$ x 4 $\frac{1}{2}$; ix + 292; 1940.

INSECT PESTS OF FARM, GARDEN, AND ORCHARD. *Fourth Edition.*

By Leonard M. Peairs. John Wiley and Sons, Inc., New York and London. \$4.00. 9 x 5 $\frac{1}{2}$; xvii + 549; 1941.

The first of these two volumes is concerned with insects that are a nuisance to human beings. The present conflict in Europe, with its evacuation problems and the herding together of military personnel and civilians has brought to the attention of public health, medical, and commercial authorities in England the importance of insect control. Part I of this handbook deals with the appearance, life history, characteristics and habits, control or eradication, etc., of the bed-bug, flea, louse, cockroach, cricket, silver-fish, ant, itch mite, book lice, earwig, wood lice, and housefly. Part II presents the techniques of fumigation with various gases, and other insect specifics, the disinfections of homes, foodstuffs and ships, with chap-

ters on legislative control and human toxicology. The volume is illustrated and indexed.

Peairs, co-author with E. D. Sanderson of the previous edition of the second of these two books (cf. Q.R.B., Vol. 7, p. 362.) has, at the request of Sanderson, assumed full responsibility for the present revision. The same general plan of presentation has been maintained but the material has been revised and rewritten to include the latest advances in the field of economic entomology. Account has been taken of the fact that changes in agricultural procedures, changes in the composition and use of insecticides, and changes in plant constitution and immunity, have drastically changed the economic importance of numerous insects; some harmful ones have become harmless or even helpful, while conversely, some quite harmless or even beneficial insects have become significant pests. The work is well documented throughout with bibliographic references, and is generously supplied with illustrations. A very useful index is appended.



ENTOMOPHAGOUS INSECTS. *First Edition.*

By Curtis P. Clausen. McGraw-Hill Book Company, New York and London. \$7.00. 9 x 5 $\frac{1}{2}$; x + 688; 1940.

Into this volume the author has brought all of the important work—and this has reached formidable proportions—which has been done on entomophagous insects. It "represents as nearly as possible, what the author himself would like to have had available while engaged in field work upon insect parasitology and the biological control of insect pests." Insects are their own worst enemies. It is estimated that about 224 families, in 15 orders, have in some degree the entomophagous habit—a fortunate habit for the present human race, since the equilibrium in the insect population is held "at a sufficiently low level to permit the existence of plant and animal life as we know it today."

Clausen, with his wide understanding of the subject, dwells less on the predator than on the parasitic insects. Predators

are those forms that usually have a free-living larval existence and require a number of hosts to bring them to maturity. Their food is usually the same in all stages. The parasitic forms develop, in the larval stage, either internally or externally on a single host individual, the latter eventually dying as a result of this relationship. The adults, almost always free-living, depend upon a different kind of food than do the larvae. The immature stages of the parasitic insects exhibit a wide range in habit and in form, growing out of the adaptations imposed by the forms and habits of their different hosts.

Fully half of the volume is devoted to the Hymenoptera, among which are to be found the most important parasites useful to man, not only as regards the number of species having the entomophagous habit but in the effectiveness with which they attack the insect pests of agricultural crops. The Diptera and Coleoptera and less important groups follow. Detailed discussions are given of host preferences, biology and habits, development and life cycle, and immature stages. Numerous figures are included in the text and the list of references covers 46 pages. A carefully planned index concludes this important text.



THE INDO-CHINESE FOREST OX OR KOUPREY. *Memoirs of the Museum of Comparative Zoology at Harvard College, Volume LIV, Number 6.*

By Harold J. Coolidge, Jr. *Museum of Comparative Zoology, Cambridge, Massachusetts.* \$3.50. 12 x 10; 115 + 11 plates; 1940 (paper).

This rare animal has only been known for about ten years. There is, or was at the time this monograph was written, a four-year-old male in the Vincennes Zoo to which Urbain has given the name *Bos (Bibos) souveli*. The present description is based on a fine specimen of an old adult bull, shot in Cambodia during the winter of 1938-39, and presented to the Museum of Comparative Anatomy at Harvard. Little is known at present about the distribution or frequency of the kouprey as

no big-game hunting has been done over the forest areas north of Cambodia.

In comparing the kouprey with the only two living kinds of wild taurine cattle from the forests of southeastern Asia, the gaur and the bantian, Coolidge finds that the "principal significant external differences by which the kouprey differs from the two others are limited to the marking of the lower legs, the peculiar horns [fringed near the tips] with their relation to the skull and the elongated tail." Detailed descriptions are given of the differences and similarities between the hides and skeletons of the kouprey, gaur, and bantian, and comparisons are made with allied genera, both living and fossil forms. "The kouprey skull, while clearly that of an Asiatic taurine, shows more primitive features than any of the other surviving forms." It is possible that further research may reveal the kouprey to be the living representative of the probable ancestor of neolithic domesticated cattle.

Seventeen tables of measurements, 10 figures and 11 plates exhibit the main descriptive features of the text. A brief bibliography for the kouprey is given and there is also a lengthy general bibliography.



ZOOLOGICA. *Scientific Contributions of the New York Zoological Society, Volume XXV, Part 4, Numbers 25-34.*

New York Zoological Society. *Zoological Park, New York.* \$2.35. 10½ x 5½; 202; 1940.

This number contains the following papers:

Eastern Pacific Expeditions of the New York Zoological Society. XXII. Mollusks from the West Coast of Mexico and Central America. Part I, by Leo G. Hertlein and A. M. Strong (2 plates); On the Electric Powers and Sex Ratios of Foetal *Narcine brasiliensis* (Olfers), by C. M. Breder, Jr., and Stewart Springer; A Study of the Activities of a Pair of *Galago senegalensis moholi* in Captivity, Including the Birth and Postnatal Development of Twins, by Florence De L. Lowther (6 plates); Diets for a Zoological Garden: Some Results During a Test Period of Five Years, by Herbert L. Ratcliffe; The Biology of the Smoky Shrew (*Sorex fumus fumus* Miller), by W. J. Hamilton, Jr. (4 plates, 1 text-figure); Social and Respiratory Behavior of Small Tarpon, by Arthur Schlaifer

and C. M. Breder, Jr. (2 plates, 1 text-figure); *New Observations on the Blood Group Factors in Simiidi and Cercopithecidae*, by P. B. Candela, A. S. Wiener and L. J. Goss; *Muscle Dystrophy in Tree Kangaroos Associated with Feeding of Cod Liver Oil and Its Response to Alpha-Tocopherol*, by Leonard J. Goss; *Mortality Statistics for Specimens in the New York Aquarium, 1939*, by Ross F. Nigrelli (3 plates); *A Comparison of Some Electrical and Anatomical Characteristics of the Electric Eel, *Electrophorus electricus* (Linnaeus)*, by R. T. Cox, W. A. Rosenblith, Janice A. Cutler, R. S. Mathews, and C. W. Coates (7 text-figures).



AMERICAN WILD LIFE. *Illustrated.*

Compiled by the Writers' Program of the Work Projects Administration in the City of New York. Wise and Company, New York. \$3.50. 9 x 5½; xiv + 749; 1940. The need for a greater appreciation and a wiser use of our natural resources has been the underlying stimulus for the preparation of this excellent volume. In its pages are found discussions on the appearances, the every-day habits, the economic value, the distribution, and the general life history of all the American chordates: i.e. mammals, birds, reptiles, amphibians, and fishes. The closing 243-page section on birds is especially good.

With the backing of the Works Progress Administration, the finished product incorporates the contributions of some fifty authorities on American natural history, and as a result, exhibits a high degree of scientific accuracy. The work is profusely illustrated, and is written in clear, non-technical language. It will undoubtedly be read and enjoyed by the general reader, as well as boys and girls of camp age.



ORNITHOLOGY LABORATORY NOTEBOOK. *For Recording Observations Made in the Field and Studies Made in the Laboratory on the Birds of North America. Fourth Edition.*

By Arthur A. Allen, with Drawings by L. A. Fuertes, M. D. Pirnie, and William Montagna. Comstock Publishing Company, Ithaca, New York. \$3.00. 10½ x 7½; vii + 204 + [32 unnumbered]; 1941.

The increased demand for a laboratory book on bird study has required the expansion of the material to render it useful to the whole United States. In this fourth edition the keys now include all orders and families of North American birds. Outline drawings of typical species are provided for the student to color, as well as outline maps for distributional data. Also in this notebook is an illustrated key to birds' nests, check lists for field trips, and Merriam's Life Zone map.



ENTOMOLOGICAL NOMENCLATURE AND LITERATURE.

By W. J. Chamberlin. Edwards Brothers, Ann Arbor, Michigan. \$2.60 (cloth) \$2.00 (paper). 10½ x 8; ix + 103; 1941. Part I of this volume presents a comprehensive history of entomological nomenclature from Aristotle, through Linnaeus and Say, down to the present International Congress of Zoology. The rules regulating the naming of new species are quoted and discussed for the benefit of new and inexperienced writers in the field of taxonomic entomology. Part II deals with the methods of assembling, filing, and the writing up of bibliographic material. This section includes also a comprehensive list of outstanding reviews, bulletins, journals, and textbooks in the general field of entomology.



THE PROBLEMS OF INSECT STUDY. *Second Edition.*

By Paul Knight. Edwards Brothers, Inc., Ann Arbor, Michigan. \$2.50. 10½ x 6½; vii + 132; 1939 (paper).

The writer states that there is nothing in this text that has not been published before. It is primarily an introductory course in entomology, based on the questions asked by a diversified group of students. For this reason many different topics are included, such as the relationship existing between plants, insects, and man; feeding, growth and embryology; adaptations of insects; distributions and

economic importance; scientific control and legislative control; the plagues and diseases due primarily to insect infestation.

A table of scientific and common names of the more numerous insects, a short bibliography, and an index are appended.



A FIELD KEY TO OUR COMMON BIRDS. *Pocket Natural History No. 8. Zoological Series No. 3.*

By Irene T. Rorimer. *Cleveland Museum of Natural History, Cleveland, Ohio.* \$1.50. 6½ x 3½; 160; 1940.

This little guide to the common birds of the north Ohio area differs from most field books in that the birds are classified according to habitats. It is doubtful whether this method is superior to the usual systematic one as birds are very often where they should not be and it is sometimes difficult to decide just in what type of territory one is observing. However, there is a field key to the species, followed by numerous small illustrations drawn by Roger T. Peterson. Verbal descriptions of the species and an appendix of uncommon birds complete this pocket size edition that can be used throughout the northeastern United States.



QUETZAL QUEST. *The Story of the Capture of the Quetzal, the Sacred Bird of the Aztecs and the Mayas.*

By V. Wolfgang von Hagen and Quail Hawkins. *Harcourt, Brace and Company, New York.* \$2.00. 9½ x 7; 198; 1939.

The quetzal is the bird held in awe by the natives of Central America because of its relation to Quetzalcoatl. Its historical and mythological interest initiated the present attempt to bring this bird back alive, a feat never before accomplished. In an extremely lucid style—the book is written for children as well as adults—the quest for the quetzal is described. The capture of the birds, and their successful rearing and transportation was due in great part to a twelve-year-old Indian boy whose keen interest in the hunt rewarded

him more than anyone ever expected. The pen-and-ink drawings are excellent.



LABORATORY MANUAL FOR INTRODUCTORY INVERTEBRATE ZOOLOGY.

By C. Courson Zeff. *The Evangelical Press, Harrisburg, Pennsylvania.* \$1.00. (Obtainable from The Athletic Store, State College, Pa.). 8½ x 5½; 55; 1941 (paper).

The outline of this manual is broad enough to meet the needs of a variety of introductory courses in invertebrate zoology. The directions generally call for drawings of the external and internal anatomy of the organism; some require cross or sagittal sections to show internal relationships; and some include detailed studies of separate parts or appendages. A note on taxonomy and terminology, and a list of references have been included.



THE TALE OF THE BULLFROG.

By Henry B. Kane. *Alfred A. Knopf, New York.* \$1.25. 9 x 6½; [47 unnumbered]; 1941.

The author has furnished not only the text but also the excellent photographs and the amusing pen and ink sketches for this delightful biography of a tadpole that grew up to be a bullfrog. Parents, as well as their children, will enjoy this book.



A BIOGEOGRAPHICAL STUDY OF THE ORDINOIDES ARTENKREIS OF GARTER SNAKES (GENUS THAMNOPHIS). *University of California Publications in Zoology, Volume 44, No. 1.*

By Henry S. Fitch. *University of California Press, Berkeley and Los Angeles.* 10½ x 6½; 133 + 7 plates; 1940 (paper).

A FIELD STUDY OF THE GROWTH AND BEHAVIOR OF THE FENCE LIZARD. *University of California Publications in Zoology, Volume 44, No. 2.*

By Henry S. Fitch. *University of California Press, Berkeley and Los Angeles.* 10½ x 6½; 22; 1940 (paper).

NOTES ON MEXICAN SNAKES OF THE GENUS *GEOPHIS*. *Smithsonian Miscellaneous Collections*, Volume 99, Number 19.

By Hobart M. Smith. *Smithsonian Institution*, Washington, D. C. 10 cents. 9½ x 6½; 6; 1941 (paper).

FURTHER NOTES ON MEXICAN SNAKES OF THE GENUS *SALVADORA*. *Smithsonian Miscellaneous Collections*, Volume 99, Number 20.

By Hobart M. Smith. *Smithsonian Institution*, Washington, D. C. 10 cents. 9½ x 6½; 12; 1941 (paper).



BOTANY

THE ADVANCE OF THE FUNGI.

By E. C. Large. *Henry Holt and Company*, New York. \$4.00. 8½ x 5½; 488; 1940.

In 1845 the potato Murrain destroyed the staple food crop of Ireland and spread "faster than cholera amongst men" throughout the British Isles and the potato growing countries of Europe. Nearly a century later, in 1939, Blight-proof potatoes were exhibited at the Royal Horticultural Society at Chelsea. Between these two events other food crop disasters occurred throughout the world. The *Phylloxera* of the vines caused such destruction in France in 1865-1872 that only the remaking of vines with root-stocks from America saved the French wine industry. The leaf rust put an end to coffee growing in Ceylon in the early '70s. In 1877 the *Saprolegnia ferax* disease spread into most of the salmon rivers of England almost as rapidly as did the potato Blight in Ireland 32 years before, and caused "consternation among gentlemen, fish-wardens and gillies." These are but four of the more spectacular epidemics of fungus diseases told about in this fascinating book.

Although interest in the fungi had begun earlier the studies were mainly concerned with nomenclature and taxonomic relationships. It was the disasters of "the famished forties" and the controversy over whether Murrain was the cause or the effect of something else, that gave

impetus to the development of the science of mycology and the research for effective fungicides. *The Advance of the Fungi* traces the discoveries in the identification of the various fungi, their life cycles, modes of transmission of plant disease, methods of control or eradication, and the personalities, both forgotten and illustrious, who contributed to our knowledge of plant pathology and epidemiology of fungus disease, and developed the science of crop defense.

The book is not only authoritative but is beautifully and wittily written. It is popular science at its best. The use of material from original scientific publications and contemporary accounts in newspapers and journals adds zest rather than dullness. The bibliography covers 26 pages, and there is an index.



PLANTS USED AS CURATIVES by *Certain Southeastern Tribes*.

By Lyda A. Taylor. *Botanical Museum of Harvard University*, Cambridge. \$2.00. 10½ x 7; xi + 88; 1940 (paper).

Whether or not Indian herbal remedies are of any medicinal value has long been a debated question and there has been little published to substantiate either side of the argument. The present work is an attempt to analyze certain of these Indian remedies in the light of our knowledge of the medicinal properties of plants. Using the author's field material, gathered from two tribes, the Choctaw and the Koasati, and supplementing it with published literature, a fairly representative group of medicines for the southeastern United States has been here assembled. The material has been organized from a botanical viewpoint with the remedies listed by family, genera and species. The most recently accepted form of plant names has been used. Under each plant is listed the tribe or tribes using it, what it is used for, the part of the plant employed, and the method of preparing and applying it. The volume also contains a discussion of the plant data assembled, a glossary of the

terms used, charts illustrating the uses of the plants, a bibliography, and a complete index.



GERMAN FORESTS. *Treasures of a Nation.*
By Adalbert Ebner. German Library of
Information, New York. Free. 10 x 8 $\frac{1}{4}$;
127; 1940.

The author is Professor of Forestry at the University of Munich and Director of the World Forestry Institute. Forestry as a science and economic enterprise originated in Germany, and in this book Ebner traces its development. He tells how the different methods of silviculture have evolved and then rejected in favor of Gayser's new theory. This theory, which has gained world-wide application, is based on the establishment of small groups of trees in mixed stands of different ages, with the idea that regeneration of a stand should be achieved by natural reproduction rather than by artificial methods. The author continues with a discussion of all phases of German forestry, including the philosophy as well as the facts.

Excerpts from German poetry and 91 beautiful photographs taken by the author add interest and beauty to this book.



A MANUAL OF AQUATIC PLANTS. *First Edition.*

By Norman C. Fassett. McGraw-Hill
Book Company, New York and London.
\$4.00. 9 x 5 $\frac{1}{2}$; vii + 382; 1940.

Aquatic plants as defined by Fassett for his purposes, are plants that may, under normal conditions, germinate and grow with at least their base in the water and are large enough to be seen with the naked eye. It is not always possible to draw a distinct line between aquatic and non-aquatic plants. A lake or river that has been at low level for some time may suddenly rise, and plants will be found in its waters that would not ordinarily be defined as aquatics. Plants growing in bogs, small woodland brooks, waterfalls,

tidal, salt and brackish waters are not included in the author's list, which, he admits, is highly subjective. The range covered is from Minnesota to Missouri eastward, and to the Gulf of St. Lawrence and Virginia. However, by no means all of the Virginia aquatics are included since Fernald is now at work on these, especially plants from the southeastern region.

An important feature of the book is the finely executed illustrations which occur on almost every page. The text is "essentially a set of directions for looking at the pictures." Part I (general key) "is based as far as possible on superficial characters for the identification of sterile specimens, and by it a plant may be run to species or genus or to family. . .". Part II contains the descriptive treatment. In an appendix is given information on the uses of aquatic plants by birds and mammals, the relation of plants to fish, and a lengthy bibliography. The volume concludes with a glossary and a well-planned index. A highly useful book for those working in this field.



PLANTS AND MAN.

By Clarence J. Hylander and Oran B. Stanley. The Blakiston Company, Philadelphia. \$3.00. 8 $\frac{3}{8}$ x 5 $\frac{1}{2}$; x + 518; 1941.

This textbook presents a survey of botany as a vital, cultural, and practical subject. Its appeal is to the general interest of the average college freshman. Its aim is to develop in students an appreciation of the importance of plants and plant products to human affairs. It provides material for a semester's course in plant science, and builds a substantial foundation for further study in botany. Clearly written, abundantly and appropriately illustrated, and well organized, the volume is divided into the following general headings: Nature of the plant world, Plants as foods and beverages, Plants as sources of wood and fibers, Plant secretions and excretions, Plants as parasites, and Enjoyment of plant life. There is no bibliography, but

a complete glossary and index are provided.



A KEY TO WOODY PLANTS *Based upon the Flora of Itasca Park, Minnesota.*

By Murray F. Buell and Robert L. Cain.
Burgess Publishing Company, Minneapolis,
Minn. \$1.00. 10 $\frac{1}{2}$ x 8 $\frac{1}{2}$; i + 30; 1940
(paper).

The detail and precision with which this key has been prepared make it a worthy contribution to the list of floral catalogues. The fact that the work is based on the trees and shrubs of Itasca Park, Minnesota, somewhat limits its range of usefulness, though it will serve well as a pattern for the preparation of keys relating to other local areas. The descriptions throughout are based on binary separations, each group being identified by the use of the same term: e.g., page 7, "c. Spines or prickles absent. . . . c. Spines or prickles present." A glossary and a check list of species included in the key are appended.



LIST OF SHRUBS EXCLUSIVE OF CONIFERS GROWING OUTDOORS IN THE BROOKLYN BOTANIC GARDEN 1940. *Guide No. 11. Brooklyn Botanic Garden Record, Vol. XXX, No. 1, 1941.*

By Charles F. Doney. *Brooklyn Botanic Garden Record, Brooklyn, New York.* 25 cents. 9 x 5 $\frac{1}{2}$; 35 + 5 plates; 1941 (paper).

Eighty-three families, 265 genera, 1021 species and 230 varieties, not including horticultural varieties of lilac and rose, are included in this list. Rehder's names have been used except in a few cases where old established names have been given with Rehder's new names in parentheses. There is an index of genera and common names.



MORPHOLOGY

EMBRYOLOGY OF INSECTS AND MYRIAPODES.
The Developmental History of Insects, Centi-

pedes, and Millepedes from Egg Deposition to Hatching. First Edition.

By Oskar A. Johannsen and Ferdinand H. Burr. McGraw-Hill Book Company, Inc., New York and London. \$5.00. 9 x 5 $\frac{1}{2}$; xi + 462; 1941.

Insect embryology has been so recently recognized as a distinct field of investigation, and the pertinent literature on the subject has been so scattered, that there has been a real need for a text wherein the basic principles, experimental techniques, and recent researches in the field could be incorporated into an organized entity. The present volume, dealing exclusively with the developmental history of insects, centipedes, and millepedes, from the time of egg deposition to hatching, fulfills this need.

The textual material, which is drawn largely from the authors' course in insect embryology given at Cornell, is presented under two general headings: I. A comparative study of the tissues and organs found in several basic types of insects; and II. The embryonic history of a number of insects so selected as to represent most of the orders. Under the first heading are included discussions on a variety of topics, such as types of eggs, cleavage, development, derivatives of the germ layers, polyembryony, parthenogenesis, and experimental embryology—the last mentioned incorporating the most recent authoritative studies on the activation and differentiation centers of the insect embryo. In dealing with the various orders of insects in Part II, the authors have been especially careful to avoid repetition of any of the material included in the preceding part.

The text is written with scientific clarity and simplicity, and is well supplied with illustrative material. Each chapter carries a list of references pertinent to the topic under discussion. Appended are a 36-page bibliography and a useful index.



THE GROWTH OF BONE, MUSCLE AND OVERLYING TISSUES AS REVEALED BY STUDIES OF ROENTGENOGRAMS OF THE LEG AREA.
Studies from The Center for Research in Child Health and Development, School of Public

Health, Harvard University, III. Monographs of the Society for Research in Child Development, Volume V, No. 3 (Serial No. 26).

By Harold C. Stuart, Penelope Hill, and Constance Shaw. Society for Research in Child Development, National Research Council, Washington, D. C. \$1.25. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; vii + 190 + [29]; 1940 (paper).

The purpose of this study was to determine the manner in which children develop in respect to the rate and the amount of growth of bone, muscle, and subcutaneous tissue, and to the variability of these two factors during the early years of life. The study was based on a series of roentgenograms of the antero-posterior view of the right leg of a group of 85 boys and 88 girls. These films were taken at specified age intervals. The techniques used in taking, measuring, and weighing of the films are described in full. The early chapters are concerned with the norms obtained from the group as a whole and the last chapter presents examples of different types of individual growth patterns. In the case studies given, family background and social, dietary, and health factors are considered briefly in relation to the principal characteristics of the growth patterns revealed. There is a bibliography but no index. The appendix contains numerous tables presenting data pertinent to the study.



A BIBLIOGRAPHY OF HUMAN MORPHOLOGY 1914-1939.

By Wilton M. Krogman. University of Chicago Press, Chicago. \$3.00. 11 x 8 $\frac{1}{2}$; xxxi + 385; 1941 (paper).

This bibliography of over eleven thousand titles deals chiefly with physical anthropology of the last quarter of a century, and as such is indispensable to all students of the human body. The author has performed an enormous and useful task in listing the work of others so that present and future students will know what information has become available and where to find it. One wonders, however, whether the bibliography of any large field of science can to-day still be collected

and arranged to general satisfaction by one man alone. If the author of the present work had called on colleagues with different interests and experiences in physical anthropology, they could have supplied the many references now omitted, could frequently have assigned titles to more appropriate sections, and, particularly could have suggested essential changes in the Outline of Contents. Last but not least, several minds, instead of only one, could more readily have eliminated the all too many minor errors which have survived proof-reading.

This bibliography, even though incomplete, may well serve as proud evidence of the astounding productivity and widespread, active interest in the morphology of man during the recent history of anthropology. It probably equals in extent the entire corresponding literature previous to 1914.



THE EMBRYOLOGY OF THE ECHIUROID WORM *URECHIS CAUPO*. *Memoirs of the American Philosophical Society Held at Philadelphia for Promoting Useful Knowledge, Volume XVI.*

By William W. Newby. American Philosophical Society, Philadelphia. \$2.00. 9 $\frac{1}{2}$ x 6; xvi + 219; 1940.

The author of this fine treatise discusses first the reproductive system and germ cells of *Urechis* and the material and methods used in the embryological investigations. In the section on the development of *Urechis* the nomenclature of cell-lineage, as modified by Conklin in 1897, is briefly explained and the zygote is carried through to the 148-cell stage. This is followed by a presentation of gastrulation and shifting of embryonic areas and axes. Finally the individual development of the various organ systems is shown. The latter half of the book is concerned with a comparison of the development of *Urechis* and that of other Echiuroidea, and a comparison of echiuroid development with the embryology of several other invertebrates. In the final section there is a discussion of the phylogenetic position of the Echiuroidea based upon embryonic characteristics.

The author concludes that echiuroids are only distantly related to the annelids. He recommends, therefore, that the Echiuroidea should be considered a separate phylum and not placed as a sub-phylum or class under the Annelida.

Eighty-five excellent figures, 4 tables of cell-lineage, a bibliography of 50 titles and a good index have been provided.



ENTWICKLUNGSGESCHICHTE DES MENSCHEN.

Zweite, neubearbeitete und erweiterte Auflage.

By Max Clara. *Quelle und Meyer, Leipzig.* RM. 13.60 (25 per cent discount outside of Germany). 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; xv + 550; 1940.

The completeness of this book makes its possession well worth while to students of human embryology. Many illustrations add to its teaching value. The heredity, spermatogenesis and oogenesis, and embryology of the frog are used as an introduction to the more complicated subject of human embryology.

The first division of the volume deals with the structure of the sex cells, fertilization, and the rôle of sex in inheritance; the second treats extra embryonic membranes, gastrulation, and processes of placentation, and the formation of ectoderm, endoderm and mesoderm; the third concerns the development of organs and organ systems.

A large bibliography is appended, and there is an index.



THE MALE GENITALIA OF HYMENOPTERA. *Smithsonian Miscellaneous Collections, Volume 99, Number 14.*

By R. E. Snodgrass. *Smithsonian Institution, Washington, D. C.* 40 cents. 9 $\frac{1}{2}$ x 6 $\frac{1}{2}$; 86 + 33 plates; 1941 (paper).



PHYSIOLOGY AND PATHOLOGY

MAN ON HIS NATURE. *The Gifford Lectures, Edinburgh 1937-8.*

By Sir Charles Sherrington. *The Uni-*

versity Press, Cambridge; The Macmillan Company, New York. \$3.75. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; 413; 1941.

This book, by the distinguished physiologist and recipient of the Nobel Prize for Medicine in 1932, was written for the Gifford Lectures, 1936-38, at the University of Edinburgh. It is a discussion of man's nature, its physiological basis, and its evolution. Sherrington takes for his text the book *On Hidden Causes (De Abditis Rerum Causis)* by Jean Fernel, physician to Henri II of France. Cast in dialogue form this treatise, first published in 1548, was within the next hundred years reissued more than thirty times and in several countries. Living in a period when magic, astrology, elixir-brewing, the philosopher's stone and the cabala all had a profound influence on human thought and behavior, Fernel's virile mind perceived that there was order and balance in nature.

"... misbalance in constitution is the illness, yet the cause is the practical point. There are causes we do not know" and again "Each animal, each plant, each mineral, whatever is in this sub-lunary world, contains a particular Nature which maintains and orders it and its kind. This particular Nature, unalterable as it is, fits with all other particular Natures." Fernel was "the earliest to draw together into one discipline physiology, calling it for the first time by that name, and holding it to be the necessary introduction to scientific medicine."

Sherrington gives a clear-cut and extremely interesting picture of the development of modern biological knowledge and the part that physics and chemistry have had in that development. Fernel's questions in the "Dialogues" he answers in the light of modern knowledge. Most of the questions are discussed in terms of the central nervous system. Concerning the problems raised by the reappearance of the mind *ex nihilo* at each repetition of the soma after the soma has reached a certain stage of ripeness, and the difficulty of interpreting mental phenomena in terms of physics and chemistry, Sherrington says:

We have, it seems to me, to admit that energy and mind are phenomena of two categories. In that case the phasic appearance of a mental system alongside the energy-system of the developing body has the difficulty that the mental seems to spring suddenly out of nothing. But we have already dealt with

instances in ourselves where mind is clearly inferable although not directly recognizable by us. If that be so in ourselves, still greater is the difficulty of observing mind objectively, that is as object, when, by its very nature, it is insensible, i.e. not accessible to 'sense'. Mind as attaching to any unicellular life would seem to me to be unrecognizable to observation; but I would not feel that permits me to affirm it is not there. . . .

The appearance of recognizable mind in the soma would then be not a creation *de novo* but a development of mind from unrecognizable into recognizable. It is at this point therefore that on these admissions we become committed to dualism. But while accepting this duality we remember that Nature in instance after instance dealing with this duality treats it as a unity. Evolution evolves it as one. In this body-mind individual, with its two cohering systems, bodily and mental, even as the former component exhibits both inherited and acquired features, so too does the latter.

With biologists becoming concerned with smaller and smaller values, it is refreshing to read the broader philosophy of such an outstanding physiologist. The volume is well printed, has a combined subject and author index and has beautifully designed title pages to each chapter. We strongly recommend this book as seminar work for graduate biology students. It lends itself admirably to discussion groups.



PHYSIOLOGIE DES SEHENS. *Retinale Primärprozesse.*

By G. von Studnitz. Akademische Verlagsgesellschaft, Leipzig. RM. 24 (cloth); RM. 22 (paper). 8½ x 5½; xii + 367; 1940.

Modern students of the physiology of vision have approached the problem from such diverse and widely separated points of view that no one worker or group of workers in this field can be said to command authority in the whole subject. Some appreciation of the diversity of the approaches to this problem may be obtained by simply listing the most important fields of study. There are, first, anatomical investigations concerning the structure of the light sensitive end organs and the neuroanatomy of the retina. This field has been extended into the submicroscopic region in respect to the retinal end organs by polarization micro-

scopy and studies on optical dichroism—techniques not regularly found in the anatomical laboratory. Far removed from these anatomical studies are those of neurophysiologists on the electrical responses of the excited retina. Here is a field of great complexity that has been diligently cultivated by a large number of workers. Equally removed from anatomical and neurophysiological techniques are those of the biologists and biochemists bent in isolating the photochemical substances primarily concerned in the response of the retina to light, and in discovering the metabolic processes by which these photochemical substances are produced. Finally, there is a large group of psychologists, ophthalmologists, and others who have studied the subjective sensory aspects of visual perception and who provide, in a sense, the raw material which the other workers attempt to explain and understand.

The centrifugal aspects of this field of science are, of course, not unique. In very many other fields similar trends have long been manifest. The conventional cure for this condition is either the organization of an institute, the creation of a commission, or the composition of a monograph. Von Studnitz has provided a workmanlike example of the third form—a monograph in which the four major fields of attack on the physiology of vision are discussed and in some respects co-ordinated. There is an excellent bibliography indicating that the subject has been competently covered.

The author's own investigations have concerned the photochemical substances of the retina. Here he exhibits himself in violent and polemical disagreement with his nearest colleagues. The reviewer does not feel competent to render a verdict on the points at issue but it is plain that the parenthetical sarcasms and abundant exclamation points, sometimes in pairs, which are scattered through this section of the book, do not add one cubit to the author's stature.



TEMPERATURE. *Its Measurement and Control in Science and Industry. Papers pre-*

sented at a Symposium held in New York City, November, 1939.

Under the Auspices of the American Institute of Physics with the Cooperation of National Bureau of Standards and National Research Council. Reinhold Publishing Corporation, New York. \$11.00. 9 x 6; xiii + 1362; 1941.

This volume presents the papers given at a Symposium on Temperature held in New York City in 1939 under the auspices of the American Institute of Physics. The subjects covered range from the temperature of the stars to production and measurement of temperatures below 1°K. Unfortunately, it is not possible in a limited space to give the salient points in the papers dealing with purely biological problems, but we give the titles of some of these (they are all by American investigators) as an indication of the important work that is being done on the effect of heat and cold on living systems.

The temperature of the human body in health and disease; The resistance of living matter to very low temperatures; The development of homeothermy in animals; Heat production and thermal conductance in small laboratory animals at various temperatures; The effects upon dogs of low oxygen tensions combined with low temperatures; Temperature factors in animal production; The temperature pattern of laboratory animals in normal and febrile states; Temperature sense in man; A new basis for cutaneous temperature sensitivity; Man's heat exchanges with his thermal environment; The operating characteristics of the human thermoregulatory mechanism; Heat loss and heat production in women under basal conditions at temperatures from 23°C to 35°C.; The significance of the average temperature of the skin; Temperature changes in the muscles of the human leg; Skin temperature of the extremities under various environmental and physiological conditions; Normal vasoconstriction vasospasm and environmental temperature; Observations on human beings with cancer, maintained at reduced temperatures of 75°-90° Fahrenheit.

Tabular matter, graphs, and references are included in each paper. The book has an author index and subject index and a valuable appendix giving the constants used in thermometry.



AUTHORITY, OBSERVATION AND EXPERIMENT IN MEDICINE. *Linacre Lecture 1940.*

By W. W. C. Topley. *The University*

Press, Cambridge; The Macmillan Company, New York. 40 cents. 7½ x 4½; 46; 1940 (paper).

In the Linacre Lecture of 1940, Topley disagrees with two of his predecessors in the unqualified praise which they bestow upon Linacre. Galen's ideas that had dominated medicine for thirteen hundred years were being replaced early in the sixteenth century by revolutionary changes of which Linacre was unaware. His translation of Galen's Greek writings into admirable Latin, to replace the corrupt versions, was a great medical achievement, but, Topley says, it can also be cited as an example of doing the wrong thing extremely well. Other men of Linacre's time were aware of the beginning of a new order in medicine. It is said that Paracelsus inaugurated his professorship at Basel, in 1527, by publicly burning the works of Galen and Avicenna. The following quotations will serve to give the reader some idea of Topley's views.

"Linacre the physician must, I think, be numbered among the authoritarians; and authority—the intellectual authority of books or men—is incompatible with science. The scientist can never regard his books as more than temporary codifications of current working hypotheses, and of the evidence on which they are based. All books, and all men, remain open to challenge, and there can be no plea of privilege.

"Medicine is not a self-sufficing entity. It is, as we know it to-day, the application to the cure and prevention of disease of knowledge and of methods drawn from a wide variety of ancillary sciences—ancillary, be it noted, only in the sense that they have services to offer to medicine, . . .

"If we could kill the last remnants of authoritarianism, abolish the false distinction between the medical scientist and the medical artist, and gain general acceptance for the view that controlled observation in the ward or in the field is an essential part of medical science, shading through almost imperceptible stages of increasing intervention into the fully developed experimental technique of the laboratory, we should, I am sure, have gone a long way to secure the intellectual sympathy and understanding that is the essential basis of fruitful common effort."



A HISTORY OF MEDICINE.

By Arturo Castiglioni. *Translated from the Italian and Edited by E. B. Krumpholtz. Alfred A. Knopf, New York. \$8.50. 9½ x 6½; xxviii + 1013 + xl; 1941.*

Confronted by a truly monumental treatise

prepared by one of the most eminent student's of the subject, it is difficult to condense within the brief space allotted the considerations which this work deserves. For Castiglioni not only delineates the development of the medical art and science but he also reveals the relation of this development to that of philosophy, science in general, and social and economic policies and ideas. Thus, the status of medicine in a certain period is made to reflect the intellectual and moral characteristics of that period. This is one of the most distinctive features of the present work. The whole recorded existence of man is covered, from the prehistoric indications of the practice of some kind of surgery to the latest discoveries concerning etiology, therapy, and prevention of disease. With respect to the medicine and surgery of our era, the author duly mentions all the well-known contemporary personalities but with a just regard for historical values he withholds comments on them. The author attributes more importance than is usually given by English students to the medical contributions of Italian physicians. To some this may seem a manifestation of chauvinism, but even though in certain cases the author's evaluation may be slightly prejudiced, it leads to a clearer conception of the evolution and dissemination of ideas more or less simultaneously in different groups. One of the noteworthy reflections made by the author concerns the evaluation of ancient Roman medicine. The author points out that, since the public hygiene and sanitation of Rome and other cities of the empire achieved a standard not equalled until modern times, it cannot be very well affirmed that Roman medicine consisted only of a pedestrian imitation of that of Greece! From the standpoint of medical science and of history this textbook undoubtedly deserves a place with the leading works on the subject.



PLAGUE ON US.

By *Geddes Smith*. *The Commonwealth Fund*, New York; *Oxford University Press*, London. \$3.00. 9 x 5½; 365; 1941.

During recent years the popularity of books that portray to the layman the advance of medical science is evidenced by the number of such publications. Many of them present the story in such dramatic style that there is some distortion of scientific perspective—personalities may be allowed to overshadow science. Such is not the case with this book, of which only the title may convey such an impression. It is a relief to read the story as it is here presented with good taste, balanced judgment and objectivity. Scientists are depicted neither as heroes nor as eccentric individuals; in fact, they are presented only as discoverers and authors.

There are seven chapters, a prologue and an epilogue. These chapters are: Pestilence, in which the problems are defined from an historical viewpoint; Past Thinking, in which is traced the development of ideas regarding the nature of contagion and infection; The Sick Man, considering the inter-relations of parasite and host; The Sick Crowd, epidemiological studies; Defenses, individual and collective; Detective Work, illustrations of diagnostic bacteriology and epidemiology in action; Unfinished Business, in which it is shown that notwithstanding the progress which has been made, much more remains to be accomplished.

The author exhibits an admirable ability to present scientific material in an interesting and understandable manner without sacrifice of accuracy and without resort to sensationalism. If, as the author modestly states, he has been much aided by the advice and criticism of friends, his friends have been well chosen.



PHOTODYNAMIC ACTION AND DISEASES CAUSED BY LIGHT.

By *Harold F. Blum*. *Reinhold Publishing Corp.*, New York. \$6.00. 9 x 5½; xii + 309; 1941.

Photodynamic action has interested many investigators since its discovery by Raab in 1893. One research worker some years ago concluded an admirable review with the remark that "there is little evidence that such sensitization plays any significant part either in the etiology or

therapy of the diseases of man." The present author, however, feels more confidence in the importance of the subject. Himself a contributor of many research papers dealing particularly with the rôle of oxygen in photodynamic action, the author devotes a major part of the first section of the book to a discussion of the factors determining photodynamic effectiveness. He also discusses at length the various theories proposed to account for the effect, although these are still in the nature of hypotheses. This material is interesting to the specialist who is actively working in this particular field.

The sections dealing with the diseases produced by light in domestic animals and in man are of more general interest. The fact that animals may become light sensitive as the result of feeding on St. Johnswort or buckwheat has long been known and frequently becomes a serious problem for the stock breeder. Sensitization of man has usually been attributed to the porphyrins and this subject is discussed very thoroughly. There is also an analysis of the relation of light to skin cancer, a subject in which there is much current interest. The book is exceedingly readable and members of the medical profession will find much to interest them in the final section.



HYGIENE. *A Textbook for College Students on Physical and Mental Health from Personal and Public Aspects. Third Edition.*

By Florence L. Meredith. The Blakiston Company, Philadelphia. \$3.50. 9 x 5½; xii + 822; 1941.

This comprehensive volume incorporates discussions of human anatomy, physiology, pathology, group biology, and personal hygiene. The predominant theme is the appropriate scientific action which is necessary to meet the health objectives arising from the health situations which exist in the lives of individuals or groups. It is essentially a new book, having been completely revised in the light of the most recent medical developments.

The opening pages give a statistical survey of mortality and morbidity in the

United States. Chapters on anatomy and physiology have been condensed from previous editions, but a valuable new section discusses the manner in which medical science may be used most effectively, warning against nostrums and quackery. Accidents and diseases, generally and specifically, are described in considerable detail, but the major portion of the volume is devoted to considerations of what the individual can do to maintain proper functioning of the various organs and organ systems. The book does not deal with general conditions of interest. It is complete and specific, written from the point of view of the physician. Although *Hygiene* is an excellent college textbook, it will find little use beyond academic doors.



THE PERIODICITY AND CAUSE OF CANCER, LEUKÆMIA AND ALLIED TUMOURS with Chapters on Their Treatment.

By J. H. Douglas Webster. The Williams and Wilkins Company, Baltimore. \$3.50.

9½ x 6½; xv + 178; 1940.

Periodicity in tumors was first mentioned by Bashford and co-workers in 1905. Since that time a number of others have found evidence that there are periods of quiescence in malignant tumors. The present studies, based on 720 cases (589 malignant cases, 42 leukaemia, 51 Hodgkin's disease, 38 benign tumors), were the result of the discovery that a patient had had breast cancer recurrences on five occasions at approximately 33-week intervals. Clinical and statistical evidence is given by Webster to show that periodicity is "a fundamental and intrinsic character of human neoplastic disease. . . ."

"The time-pattern which has been found is not a simple one (or it would have been discovered long ago); it has a triple *facies*, showing itself as full, half, or 'missed' periods; the standard full-period being 33 weeks, as in influenza."

It was found that treatments (surgery or radiotherapy) would postpone or abolish the appearance of the periodicity, but the rhythm was not altered. Webster believes that the periodicity of cancer and

the rare instances of contagion lend support to more direct evidence of the virus causation of tumors.



BIOLOGICAL ASPECTS OF INFECTIOUS DISEASE.

By F. M. Burnet. *The University Press, Cambridge; The Macmillan Company, New York.* \$3.75. 8½ x 5½; vii + [5] + 310; 1940.

The point of view from which the author discusses infectious diseases is that of the ecology of the pathogenic parasite. He seeks to make it clear that parasitic diseases represent certain kinds of reactions between man and other organisms, and that these organisms are subject to the same natural laws which regulate all living matter. In some detail the author describes first the kinds of parasites: bacteria, viruses, etc. He then proceeds to delineate the interaction between the parasite and man in terms of disease resistance and immunity, and epidemics. Separately, the author treats of some of the more important infectious diseases—diphtheria, influenza, tuberculosis, plague, cholera, malaria, and yellow fever—with an account of their etiology, incidence, and epidemiology. Although the book is apparently written for the non-biologist, it deserves to be read and pondered by all who are interested in medical sciences. An exception could be taken to the title since the author omits any but the most indirect mention of the biology of the host, man.



TEXTBOOK OF HEALTHFUL LIVING. Second Edition. By Harold S. Diehl. *McGraw-Hill Book Company, New York and London.* \$2.75. 8½ x 5½; x + 634; 1939.

In its original form the volume was written for the general reader. The carry-over of this method of presentation seems to limit the usefulness of the present edition as a textbook. Major topics discussed are the present situation regarding health and longevity, nutritional

and digestive considerations in the maintenance of health, the relationship of the individual to his physical environment, and immunization. Somewhat more specific are chapters describing the care of teeth, throat, nose, ears, and eyes. General treatment is accorded to sex life, mental health, and diseases of advanced age, while the closing chapters discuss public health services. Very little space is given to anatomy or physiology, since the author considered these subjects as being "only remotely related to the practice of personal hygiene. . . ." This still remains a good book for the general reader, but will be most useful in college courses as a source of supplementary information. The volume contains many good references and is thoroughly indexed.



STUDIES ON TUBERCULOSIS. *The American Journal of Hygiene Monographic Series, No. 16, February, 1941.* Containing the following: *The Spread of Tuberculosis in Negro Families of Jamaica, B.W.I.,* by E. Joyce Saward, Persis Putnam, and Eugene L. Opie; *The Fate of Negro Persons of a Tropical Country, Jamaica, B.W.I., after Contact with Tuberculosis,* by Eugene L. Opie, Persis Putnam, and E. Joyce Saward; *A Survey of Tuberculosis Infection in a Rural Area of East Alabama,* by A. H. Graham, P. W. Auston, and Persis Putnam; *The Fate of Persons Exposed to Tuberculosis in White and Negro Families in a Rural Area of East Alabama,* by A. H. Graham, P. W. Auston, and Persis Putnam.

The Johns Hopkins Press, Baltimore. \$1.10. 9 x 5½; 198; 1941.

Although presented separately, these four papers are so closely interrelated that the volume is essentially a monograph. In general the authors conclude that tuberculosis runs a shorter, sharper course, and more frequently ends fatally in Negroes than among whites, and that there is a higher frequency of latent tuberculosis among whites. Data on the development of secondary cases in family groups after the removal of active cases from those groups are also presented. Two family

charts are given as illustrations at the end of the book.



MEDICINE AND HUMAN WELFARE.

By Henry E. Sigerist. Yale University Press, New Haven; Oxford University Press, London. \$2.50. 8 x 5½; xiii + 148; 1941.

One theme dominates the pages of this book: namely, that throughout history the medical treatment of the working classes has been inadequate. Sigerist describes the intimate relationship between medicine and social changes from earliest times, showing how we have come to accept the view that all classes are deserving of equal medical attention, and how at the same time we have neglected to carry out this policy. It is true that within recent years the socialization of medicine has progressed rapidly, but, according to Sigerist, it is limited by an adverse and inadequate economic system.

The book presents a broad health program for every country, one aspect of which must be the freedom of the physician from the sphere of competitive business. It is further emphasized that scientific medical research is not enough. It must be supplemented by sociological investigations.



FAMOUS RECIPES BY FAMOUS PEOPLE.

Compiled and Edited by Herbert Cerwin. Illustrated by Sinclair Ross. Lane Publishing Co., San Francisco, California. \$1.00. 9 x 6½; 62; 1940.

Among the famous people who are contributors to this interesting recipe book are Julian Street, whose "spinach in coated pellets" may possibly make some friends for this unpopular vegetable; Kathleen Norris whose "crab Creole romantique" is more than *romantique*; Gertrude Stein, whose "chowder Alice B. Toklas" is as complicated to concoct as her writings are to comprehend; Irwin Cobb, whose "southern hash" is worthy of a banquet; and many chefs, whose dishes have made restaurants famous. However, the con-

tribution which most takes our fancy is by the anthropologist and explorer Hrdlicka:

The front quarter of a sheep, roasted slowly over hot embers, under a studded sky, in a semi-desert, with but a native or two about, and the mules or horses; with the night deepening around, the earth resting, and the worlds beginning to talk to each other.



DEUTSCHE WISSENSCHAFT IM KAMPF UM DIE HEILUNG DER TUBERKULOSE. *Vorschlag zur Gründung eines Deutschen Tbc.-Therapie-Forschungsinstitutes.*

By Wilhelm Pfaff. Georg Thieme Verlag, Leipzig. RM. 1.20 9½ x 6½; 32; 1941 (paper).

In 1933 the author gave an account of his work on the care and cure of the tuberculous in a monograph *Der Aufbau der Tbc. Therapie als wissenschaftliches und staatliches Problem*. This is summarized briefly in the present study, and the results of further work reported. Some of his experiments on animals were unsuccessful and could not be carried out satisfactorily because systematic investigations in this direction needed a broader basis. The author therefore suggests the foundation of a German Therapeutic Research Institute for Tuberculosis, with four interdependent divisions: pharmacological, pathological-anatomical, bacteriological and hematologic-serological, and chemical. The duties and problems of the four divisions are outlined briefly.



MICROBIOLOGY AND PATHOLOGY. *Fifth Revised Edition.*

By Charles G. Sinclair. F. A. Davis Company, Philadelphia. \$3.25. 8½ x 5½; ix + 393; 1940.

It seems particularly desirable to present bacteriology, the study of viruses, protozoology, mycology and parasitology in the form of one subject—microbiology. It is also desirable to relate pathology to microbiology. The present volume, an elementary text for nurses, dieticians, and for those engaged in physiotherapy and occupational aids, is of necessity broad in

scope. It therefore suffers from the difficulties that any book of this type encounters. However, the book is well planned and in spite of some inaccuracies due to over-simplification and the fact that the bacteriological terminology is archaic and inconsistent, it has fewer faults than others in the same field. The volume is well illustrated and is indexed.



HOW TO PREVENT GOITER.

By Israel Bram. E. P. Dutton and Company, Inc., New York. \$2.00. 8 x 5½; 182; 1941.

It is estimated that over 7,000,000 Americans suffer from goiter and glandular diseases. In this volume a medical authority dispenses pertinent preventive information for the lay reader. The book is not offered in any way as a substitute for the physician. It is the purpose of the author to set forth the simple rules of physical and mental conduct that will help to prevent disturbances of the thyroid gland. He discusses in order: the rôle of the thyroid in life's processes; the healthy and unhealthy thyroid; causes and varieties of goiter; goiter "belts"; the prevention and treatment of simple and exophthalmic goiter; and the effects of eating, sleep, and thinking on the thyroid gland. The book is illustrated with representative cases. There is an index, but no bibliography.



THE COMPARATIVE PHYSIOLOGY OF RESPIRATORY MECHANISMS.

By August Krogh. University of Pennsylvania Press, Philadelphia. \$3.00. 9 x 5½; vii + 172; 1941.

This book presents the subject from the comparative viewpoint, and, therefore, is a valuable addition to our texts on respiration. The author has collected numerous facts concerning the respiratory activity of many types of animals and discusses their need for oxygen and their mechanism for meeting this need. Since a large amount of this work has been done by Krogh and his assistants, the

book is mainly a first-hand account of these researches. It is an admirable presentation of the ability of animals to adapt their respiratory mechanisms to environments of air or water. The work contains a list of references, an index of animals mentioned in the text, and a subject index.



THE MACHINERY OF THE BODY. Revised Edition.

By Anton J. Carlson and Victor Johnson. The University of Chicago Press, Chicago. \$4.00. 8½ x 6; xix + 620; 1941.

A revised edition of a popular college text on physiology. New material has been incorporated in the chapters already published and a new chapter on reproduction has been added. The clarity of presentation of the text and the excellence of the illustrations make this book valuable for college students desiring to understand the basic functions of the human body. There is a good subject index and a short list of selected references.



DIE GESCHICHTE DER SCHWINDSUCHT.

By Richard Bochall. Georg Thieme Verlag, Leipzig. RM. 4.80; RM. 3.60 (outside of Germany). 9½ x 6½; 73; 1940 (paper).

Written primarily for medical students, this history of studies on, and theories concerning, phthisis and the treatment of patients, begins with pre-Hippocratic times and ends with the seventeenth century, i.e. Harvey, Paracelsus, Konrad Schneider, Malpighi, and their medical contemporaries. It is adequately annotated, and there is a bibliography but no index. A second part, to treat the history of pulmonary tuberculosis, is planned.



SPITAL UND ARTZ VON EINST BIS JETZT.

By Richard Goldbahn. Ferdinand Enke Verlag, Stuttgart. RM. 8 (cloth); RM.

6.40 (paper). 9 $\frac{1}{8}$ x 6 $\frac{1}{2}$; viii + 188; 1940 (paper).

A well-written, brief, and at times intentionally sketchy, history of the development of medical practice and hospital services from antiquity to the present day. An appendix discusses watering-places and bath cures. A fairly lengthy bibliography is arranged under various headings, such as Middle Ages, epidemics, modern times, treatment of the insane. Illustrations add interest to the volume.



BIOCHEMISTRY

THE CHEMICAL ACTION OF ULTRAVIOLET RAYS.

By Carleton Ellis and Alfred A. Wells. Revised and Enlarged Edition by Francis F. Heyroth. Reinhold Publishing Corporation, New York. \$12.00. 9 x 6; ix + 961; 1941.

The familiar work of Ellis and Wells, published under this title in 1925 by the Chemical Catalog Company, has been greatly enlarged in this revision and somewhat extended in scope. As the book in its original form is well known to workers in the field of photochemistry a comparison of the original text with the revised edition will perhaps give the clearest idea of the new text.

In the section on sources of ultraviolet radiation there is a new chapter on the emission of radiant energy which is a valuable addition, and there is also much new material on the carbon arc, solar radiation, and ultraviolet transmitting glasses and filters which makes the revised text a far more inclusive reference book than the earlier one. It seems unnecessary, however, to devote three chapters to details of the construction and operation of mercury vapor lamps. This material could have been condensed with advantage.

In the second section on photochemical processes there are several valuable new chapters on the mechanism of photochemical processes and a very inclusive summary of photochemical reactions. The great body of new material in this field since 1925 makes this section particularly interesting.

The section on applications of photochemistry to industrial products is largely new material as this topic was touched on only very briefly in the earlier text.

Like all the other sections the part on applications of ultraviolet radiation in biology has been very much expanded due, naturally, to the large volume of work that has been done in this field since 1925. While the chapter on the photochemical behavior of compounds of biological interest is very significant and most appropriate for inclusion it seems to the reviewer that this section as a whole could have been condensed with advantage by including only those biological effects of ultraviolet radiation which can be clearly related to definite photochemical changes. The author states that this was his intention but the material could have been more restricted with advantage.

The book will serve as a valuable reference work in photochemistry and the only criticism found is the fact that in an effort to make the material inclusive for workers in both chemistry and biology the author has made the book unwieldy in length. The new material added in Parts II and III is extremely important and much of it is not readily available elsewhere. The material in Parts I and IV that has been adequately reviewed in other publications might have been cut to a minimum with advantage. But the book as a whole will be very valuable to photochemists and more than fills the need for a revision of the earlier book which is now so completely out of date.



DIE METHODEN DER FERMENTFORSCHUNG. Lieferung 5.

Edited by Eugen Bamann and Karl Myrbäck. Georg Thieme Verlag, Leipzig. RM. 42. 11 x 8; 1277-1836; 1940 (paper). A further contribution (cf. Vol. 15, p. 503 and Vol. 16, p. 239 for notices of the earlier numbers) to a comprehensive series on methods of enzyme investigation presented by some of the foremost workers in their field. In the present number Part I of the entire study is concluded and Part II begun. The continuation of Part I presents: (a) general methods of preparing

algae, yeasts, molds, protozoa, embryonal tissues, and adult tissues for enzyme analysis; (b) general methods of enrichment and separation of enzymes, chromatography, foam analysis, and electrophoresis; (c) methods for determination of the more general characteristics of biological catalysts. The effect of radiation and heavy water on fermentation are also discussed. In the section of Part II included in this number more particular attention is paid to the preparation, analysis, and properties of the purified hydrolases and carbohydrases. Unfortunately, the bibliography will not appear until the end of the completed series.



THE BIOCHEMISTRY OF SYMBIOTIC NITROGEN FIXATION.

By Perry W. Wilson. *The University of Wisconsin Press, Madison.* \$3.50. 9 x 5½; xiv + 302; 1940.

This monograph has been prepared as a sequel to *The Root Nodule Bacteria and Leguminous Plants* by E. B. Fred, I. L. Baldwin, and Elizabeth McCoy, published in 1932. At that time "the chemistry of symbiotic nitrogen fixation was a relatively unexplored field." The present volume presents in a readable manner the extensive studies the author and others have contributed to the subject since the publication of the earlier one. It gives a broad chemical approach to the knowledge of the Leguminosae and the complex relationship existing between symbiotic bacteria and plants, including the relevant vitamin complexes, bacteriophage, auxins, photochemistry, secretory mechanisms, the pN_2 and pO_2 functions, and isotope tracer results. An up-to-date cross-indexed bibliography completes this book, which should prove useful to biologists and agriculturists as well as to workers in the specific field.



IF THEY COULD SPEAK!

Chilean Nitrate Educational Bureau, 120 Broadway, New York. Free. 7½ x 5½; 56; 1941 (paper).

Ninety-five kodachrome illustrations, showing results of mineral deficiency (boron, calcium, copper, iron, magnesium, manganese, nitrogen, potash, and zinc) in 34 grains, vegetables or fruits, make up this little book. Each plate is accompanied by a descriptive identification.

It is suggested that the correct use of such natural fertilizer materials as Chilean nitrate of soda, which contains these necessary elements as impurities, will prevent the development of plant food-deficiency diseases. It is not claimed, however, that it is a cure-all which will promptly correct a deep-rooted condition resulting from long neglect.



WHAT ARE THE VITAMINS?

By Walter H. Eddy. *Reinhold Publishing Corp., New York.* \$2.50. 9 x 6; [8] + 247; 1941.

Today everyone is conscious of the importance of vitamins, but few people have a reliable knowledge concerning them. The content of this book answers the query in the title. A brief history of the subject is followed by a discussion of the probable function of vitamins as necessary factors in cellular respiration and metabolism of specific tissues. In succeeding chapters the vitamins are dealt with letter after letter as to the physiological manifestations of deficiency consequent upon histological changes. In each case methods are explained for diagnosing the deficiency, and the normal requirements are given when known. The author reviews the most authoritative literature on each subject, presenting an extensive bibliography. In the appendix the chemical composition and properties of vitamins are given, and also a table of vitamin units, by weight and portion, found in foods. For biologists and physicians the book will be highly useful, but the specialized medical and chemical terminology will preclude any service to the masses.



MECHANISMS OF BIOLOGICAL OXIDATIONS.

By David E. Green. *The University*

Press, Cambridge; The Macmillan Company, New York. \$2.75. 8½ x 5½; 181; 1940.

This compact volume is a welcome change from the lengthy presentations that are so often characteristic of enzyme literature. In a concise and systematic manner the author presents the most recent facts and interpretations of enzymatic oxidations, particularly of those systems where the pure enzymes or prosthetic fragments have been used in the studies. The prosthetic groups containing copper, iron, zinc, flavin, nicotinamide, thiamine, and glutathione are particularly discussed. References are provided with each chapter and there is an index. A stimulating, clearly-written book for thinkers in this field.



THE THEORY OF ORGANIC CHEMISTRY. *An Advanced Course.*

By Gerald E. K. Branch and Melvin Calvin. *Prentice-Hall, New York.* \$4.00. 9 x 5½; xix + 523; 1941.

A good fundamental and methodological approach to theoretical organic chemistry, presenting the most basic concepts of classical structural chemistry, of physics, and wave mechanics. The authors, realizing the state of flux of modern chemical concepts have presented their own views on the subject, and confined other views for the mechanisms discussed to very brief treatment. The nomenclature used is that felt by the authors to be the most clear and permanent. Advanced students of organic chemistry and molecular structure will find this book well worth reading.



PHOTOSYNTHESIS.

By E. C. C. Baly. *D. Van Nostrand Company, New York.* \$4.75. 8½ x 5½; vii + 248; 1941.

After describing the more important characteristics of photosynthesis, the author presents a detailed account of investigations of this process carried on in his own laboratory. The author believes that his investigations have led in the end to the photosynthesis in the laboratory of

carbohydrates from carbon dioxide and water. Although careful workers here and abroad have not been able to confirm this feature of Baly's work, his own account of his experiments will interest students of photosynthesis.



MAGIC IN A BOTTLE.

By Milton Silverman. *The Macmillan Company, New York.* \$2.50. 8½ x 5½; xi + 332; 1941.

The history of ten pharmaceuticals has been told by Silverman in the form of stories about the men who made them available. The subjects range from morphine and quinine to the barbitals and sulfanilamide, and from the vitamins to the hormones. The author has left no "microbe's eyelash" unturned in his search for dramatic incidents, yet each narrative is true to the facts.



SEX

REPORT OF THE COMMISSION ON MIXED MARRIAGES IN SOUTH AFRICA.

Commission on Mixed Marriages, Union of South Africa. Government Printer, Pretoria. 3s. 13 x 7½; 56; 1939 (paper).

The Commission was established to inquire whether marriages between Europeans and non-Europeans were (a) on the increase or likely to be, and (b) sufficiently numerous to be detrimental to the welfare of the Union, and "whether any further steps should be taken to discourage such marriages." Although the questions appear to the naive observer to be straightforward, this report concerns itself in great part with accounts of the miscegenation and immorality between the white settlers and the natives, the history of the marriage laws in the Union, and a summary of the marriage laws of the United States barring marriages between white and colored. So far as answering the above questions one is given a beautiful illustration of indirectness and prejudice. The official data on marriages between Europeans and non-Europeans show that there has been a decrease in such

unions. However, with justice the Commission points out that the data may not be accurate because some non-Europeans pass or are allowed to pass as Europeans. Therefore, no answer is given to question (a). Apparently the majority of the Commission voted yes to the first question under (b) mainly because miscegenation creates social problems. The Commission also voted yes to the second question. Exception to the Commission's conclusions was taken by one member, Mrs. Nellie Brown Spilhaus, M.P.C. She deserves to be mentioned because her comments, two pages long, represent a real attempt at an intelligent unbiased evaluation of the problem. If the Union of South Africa was seriously desirous of studying this important question it would seem that either the government or the local geneticists or both muffed the opportunity for some worth-while research.



THE WONDER OF LIFE. *How We Are Born and How We Grow Up.*

By Milton I. Levine and Jean H. Seligmann. Simon and Schuster, New York.

\$1.75. 8 x 5½; 114; 1940.

This excellent presentation of modern sex hygiene is a tribute to the ingenuity of its authors—one a pediatrician and the other an educator. It has been written for preadolescents and adolescents in a clear, straightforward manner, avoiding all the sentimentality so often associated with books of this nature, and without offending the intelligence of its youthful readers. It gives clear, concise and simple descriptions of the male and female sex organs, the processes of puberty and related sexual changes, pregnancy, childbirth, and lactation. Additional chapters discuss twins, triplets, quadruplets, and quintuplets, family resemblances, and "the wonder of life." The illustrations and diagrams are particularly noteworthy and commendable. There is neither a bibliography nor an index, but a glossary of terms has been included.

BIOMETRY

TABLES OF RANDOM SAMPLING NUMBERS.
Tracts for Computers No. XXIV.

By M. G. Kendall and B. Babington Smith. The University Press, Cambridge; Macmillan Company, New York. \$1.75. 9½ x 6½; x + 60; 1939.

This publication constitutes a supplement to No. XV of *Tracts for Computers* in which L. H. C. Tippett published a list of 40,000 "random numbers." The authors formed and tested for randomness 100,000 additional numbers. Since the numbers prepared by Tippett have proven their usefulness, the present series is a desirable addition to the statistical literature. Anyone who has the task of arranging any set of items in random order will find this publication useful. This reviewer has, in the past, found it advantageous to punch a number from Tippett's table on each Hollerith punched card carrying biometric data, in order that a random sub-set might be readily available. The longer series of random numbers will be very helpful in problems of this type.



THE BULLETIN OF MATHEMATICAL BIOPHYSICS. Volume 3, Number 3, September, 1941.

Edited by N. Rashevsky. University of Chicago Press, Chicago.

This number contains the following papers: Electrical Charges and Potentials in Cells Resulting from Metabolism of Electrolytes, by Robert R. Williamson; Note on the Mathematical Biophysics of Temporal Sequences of Stimuli, by N. Rashevsky; A Note on the Nature of Correlations Between Different Characteristics of Organisms, by N. Rashevsky; Mathematical Biophysics of the Galvanic Skin Response, by Clyde H. Coombs; A Theory of Steady-State Activity in Nerve-Fiber Networks: II. The Simple Circuit, by Alston S. Householder.



PSYCHOLOGY AND BEHAVIOR

MIND THROUGH THE AGES. *A History of Human Intelligence.*

By Martin Stevers. Doubleday, Doran

and Company, New York. \$3.75. 9 x 5½; xii + 521; 1940.

Those who have read Ridpath's *History of the World* will recall that it consisted chiefly of lists of kings and battles. When this work was written in the last century kings were still considered the most significant personages in history, and battles its most decisive events. But a great deal of water has flowed under the bridge since Ridpath dropped his pen, as those who compare the present work, written a half-century later, may see for themselves. Today we realize that kings are mostly figure heads for "mayors of the palace," and that questions decided on the field of battle generally do not stay settled.

To the author of the work now under consideration it seems clear that the important events in human development have been thoughts. Whenever the course of history has been changed it is because somebody had an idea. The great revolutionaries have always been, and must always be, the great thinkers. To understand man it is necessary to understand what and how and why he thinks.

The present book is a history of human mentality. It begins with the origin of human intelligence, as nearly as that can be appraised on the basis of the psychology of babies, primates other than man, and our knowledge of the pleistocene submen. It then traces the development of intelligence through the archaeological and historical records to the present. In its pages we meet Hammurabi, Ikhnoton, Assur-bani-pal, Nabopolassar, and all the other thinkers of antiquity, as well as their successors and representatives in later ages, and learn just what they contributed to modern thought.

Four appendices cover respectively human raciation, the correlation of dates in ancient history and the establishment of those in pre-history, the growth of the alphabet, and the neolithic men of Europe, explaining in detail matters that are too often neglected in works of this nature.

The illustrations are good but they are altogether too few. The twenty-five page index is very comprehensive. The profundity of thought and the lucidity of its style combine to make this a truly great

book that is likely to grip the reader's attention until he has read it from cover to cover.



PRINCIPLES OF ABNORMAL PSYCHOLOGY:
The Dynamics of Psychic Illness.

By A. H. Maslow and Béla Mittelmann.
Harper and Bros., New York and London.
\$3.50. 8¼ x 5½; x + 638; 1941.

The foreword of this book states that it is an attempt

to present an integrated picture of what we know of the psychologically disturbed individual. In this attempt we have used contributions from a wide variety of sources—from clinical, experimental, hypnotic, comparative, psychoanalytic, and psychobiological observations. Our aim was to avoid polemics and to utilize and synthesize whatever good material was available. We have brought to this task two traditions that are certainly ready for fusion, namely, the experimental-academic and the clinical-medical.

The book is divided into five parts. The first, Introductory concepts, concisely describes the present-day concepts of the "person as a whole," with adequate attention to complaints which may arise at any level of integration. The second part deals with psychodynamic processes which again are presented clearly with avoidance of technical language. The concepts presented deal with the individual in his attempts to make an adjustment to his environment. There is an interesting chapter on experimental behavior disturbances. The etiology of psychopathology is next discussed from the points of view of heredity, of cultural and social factors, and finally from the individual's own experiences, particularly in the parent-child relationship. In the section on therapy the various techniques commonly spoken of are described, with discussion of the methods and aims of each. The final section is a description of the various symptom syndromes, stressing Meyer's view of reaction types and pointing out the impossibility of rigid classification systems. The reactions are described in the conventional terminology with interesting case presentations.

There is a lengthy bibliography (819 references) in addition to the reference notes at the end of each chapter pointing

out the most pertinent references and the ground that each covers. Appendix I describes briefly various examination methods including the Rorschach test, play technique and the Murray thematic apperception test. A second appendix gives statistics bearing on the magnitude of the problem of mental disorder in the United States. The book is well indexed and contains a glossary.



STUDIES IN INFANT BEHAVIOR. V. *University of Iowa Studies in Child Welfare, Volume XVI, Number 2.*

By Ruth K. Lederer and Janet Redfield.
University of Iowa Press, Iowa City, Iowa.
\$1.35 (cloth); \$1.00 (paper). 9½ x 5½;
157; 1939.

The first of the two studies which comprise this volume is concerned with the handed status of children during the first two years of life. A critical review of the literature forms an introduction to the body of carefully organized observations. Wherever possible, the data have been tested for statistical significance, and have been discussed in the light of such analysis. This investigation points to the general conclusions that: (1) between the sixth and eleventh month, there are about equal numbers of right- and left-handed cases; (2) changes in handed status occur more frequently during the first year of life than in the second; and (3) there is a tendency for changes to occur more frequently from left-handed status than from right. As a result of the exploratory nature of the investigation, the conclusions are admittedly tentative, requiring confirmation by further investigations along various suggested lines of approach.

The second study deals with the response of new-born infants to varying degrees of light intensity. In this, the accepted conclusion that light has an inhibitory effect upon the bodily activities of infants is confirmed, and is extended to include the observation that the inhibition is progressively greater as the intensity of light is increased.

Both studies are supplied with tabular

matter and lists of bibliographic references.



THE PHILOSOPHY OF SILENCE.

By Alice B. Greene. Richard R. Smith,
New York. \$2.50. 8½ x 5½; xi + 254;
1940.

The author of this book states that her purpose has been "to examine into the practice of silence as observed in many different climes and times, and to do this in the scientific spirit. . . ." She states: "Much is required of . . . the aspirant to first-hand knowledge of the wider reaches of his own being and the larger realities to which it can lead." This statement suggests the, what seems to this reviewer, unfortunate dichotomy which pervades the book, namely the "supernormal experiences" of man in contrast to his materialistic satisfactions. Two types of silence are recognized—reflection of scientific thinking which is usually concerned with external problems, and religious meditation which attempts to push back "inner frontiers" and the "invisible sources" of life—"the larger life," "rebirth," "transformation of the self," etc. The author states: "The practice of the religious type of silence necessitates a progressive stilling of the physical, emotional and mental areas . . . a cleansing of subconscious areas." It is to this latter type of silence that eight of the ten chapters of this book are devoted. The material assembled is largely historical and was gathered in preparation for the author's doctoral thesis at Columbia University. The handling of the subject matter is in the evangelistic rather than scientific spirit. There is a bibliography and an index.



THE ADOLESCENT PERSONALITY. *A Study of Individual Behavior.*

By Peter Blos. D. Appleton-Century Company, New York and London. \$3.00.
8½ x 5½; xiii + 517; 1941.

This book presents a study of adolescents which is of great interest both in itself

and in the concepts delineated. It is essentially a study of personality reactions as reflected in the individual's performance record and his behavior under different circumstances, with emphasis on the meaning of what he says and does in the light of his personality organization. The approach used is that of the case-study. The book is divided into five sections. In the first section certain fundamental concepts are given and the case-study approach is discussed. In the second section two case studies, one of an adolescent school-girl and one of an adolescent school-boy, are presented in detail. Based on this type of material, a theory of adolescent development is discussed in the third section. The goals of adolescence are formulated as three-fold: emancipation from the family, heterosexual adjustment, and vocational, ideational, and economic self-determination. Adolescent behavior is seen as experimental and protective in character, bearing the signs of temporary adaptive efforts toward these goals. In the fourth section two case studies of an out-of-school adolescent girl and boy are given. The final section is devoted to a discussion of education and adolescent development.

A list of references is given at the end of sections one, three, and five, and there is an index. A sound, factual, thought-provoking contribution to the literature on adolescence.



THE NINETEEN FORTY MENTAL MEASUREMENTS YEARBOOK.

Edited by Oscar K. Buros. Mental Measurements Yearbook, Highland Park, N. J. \$6.00. Ten percent discount given on all orders sent directly to the Mental Measurements Yearbook. 10½ x 7½; xxiii + 674; 1940.

This book represents a very complete and successful attempt by 250 of the leading psychologists, teachers, and test technicians to review the huge numbers of tests available for measuring various human qualities and abilities. The reviews are frankly critical and one is given definite

indication of what value the reviewer considers the test and what its use should be. The subject matter covers tests on character and personality, achievement batteries, educational subjects such as languages and mathematics, a miscellaneous section having to do with such widely diversified interests as religion and agriculture, science, social studies, and vocations. To this mass of material is added a collection of various reviews that have been accorded books related to this general subject during the past year. These are instructive and very interesting as the opinions are often sharply conflicting. The price of each test and book and where it may be obtained is added.

In the section on character and personality tests there is an excellent bibliography concerning the Rorschach test but nothing concerning the test itself. One also misses reference to Murray's thematic perception test, a test which is coming more and more into clinical use.



A FIELD STUDY IN SIAM OF THE BEHAVIOR AND SOCIAL RELATIONS OF THE GIBBON (HYLOBATES LAR). *Comparative Psychology Monographs, Volume 16, Number 5, Serial Number 84.*

By C. R. Carpenter. With an Introduction by A. H. Schultz. The Johns Hopkins Press, Baltimore. \$2.00. 10 x 6½; 212; 1940 (paper).

This monograph presents a graphic account of a field trip made by the author over a four-month period in 1937 to Siam to study the gibbon in its natural habitat. The project is described as "a systematic naturalistic study by observational and recording methods of the ecology, behavior and social relations of the gibbon, *Hylobates lar*, in its natural environment in Siam." The material comprised in this monograph is presented in precise and interesting fashion. In the introduction the place of the gibbon among the primates is discussed by Adolph H. Schultz. Chapter I describes the objectives and organization of the expedition

itself. In the following chapters observations made on individual behavior, population, intragroup social relations, territoriality and inter-group relations, and group coordination, control and integration are reported. The final chapter contains a general summary of the main points noted. There is a bibliography of 103 titles and an index.



COURTSHIP AND DISPLAY AMONG BIRDS.

By C. R. Stonor. *Countryside Life, Ltd., London.* 8s. 6d. net. $8\frac{1}{2}$ x $5\frac{1}{2}$; xv + 140; 1940.

Birds are well known to have spectacular and intricate displays of infinite variations, each species with its own individual pattern. To describe all these performances would be impossible in anything but a monumental compendium. The author has therefore chosen some of the more complex and better known displays for those interested in natural history and for ornithologists who have not had time to go deeply into this branch of the subject.

Stonor believes that form preceded function and arose by variations that were selected for their greatest use and that these were converted through the ages to their present form. This idea he illustrates by examining closely the behavior of several closely related birds (the birds-of-paradise) and correlating differences in their behavior pattern with their morphological peculiarities.

The illustrations are excellent and show to what extent bird photography has progressed. Altogether this is a good review of a complicated phase in the behavior of birds and should be of interest to all biologists.



THE PERSONALITY OF ANIMALS.

By H. Munro Fox. *Allen Lane, Penguin Books, Harmondsworth.* 6d. 7 x $4\frac{1}{2}$; 123; 1941.

Most of us, in expressing opinions about the minds of animals, assume that the animal's mentality is a simpler edition of

our own. The scientist, however, will permit himself to assume nothing; he investigates the animal's mind just as he does the animal's breathing or digestion—by experimentation. In the present book, Fox gives, in clear and non-technical language, the biologist's point of view on the senses, the mind, and the personality of animals, together with the most important recent results of scientific investigations. Subjects discussed include: the animal's world; how animals communicate; what some animals can hear and what colors they can see; play; animals that find their way home; can animals count?; social rank, instinct; and intelligence. The conclusion reached is that "those animals which have the fewest instincts possess most personality." The series of sixteen illustrative plates is very well chosen. The book contains neither bibliography nor index.



A WATERHEN'S WORLDS.

By Eliot Howard. *The University Press, Cambridge; The Macmillan Company, New York.* \$2.50. 10 x $7\frac{1}{4}$; vii + 84 + 2 plates; 1940.

From careful observations of the breeding habits of the waterhen, the late Eliot Howard again demonstrates his keen analytical interpretations of animal behavior. The worlds of the waterhen are said to consist of the territory world, the sexual, the platform, and the family. These worlds are not separate entities, but form part of a connected whole, and, in the breeding cycle, necessarily follow in chronological order. Howard feels sure that birds have feelings that are expressed in action but that these two are concomitant as there is no feeling without action and no action without feeling. The internal physiological state of the individual which changes from day to day, has a bearing on the bird's activities.

This book is recommended only to a serious reader for it is not easy to follow the author's argument. It is a notable contribution by a great observer who was

a pioneer in the modern study of bird behavior.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

RELIGION IN SCIENCE AND CIVILIZATION.

By Sir Richard Gregory. *The Macmillan Company, London and New York.* \$3.00.
8½ x 5½; xiii + 366; 1940.

The author of this work tells us that religion, like Gaul, is divided into three parts—theology, worship, and ethics. The first of these to emerge in human evolution was worship, which originated as a ritual of taboos for the purpose of coercing the personified forces of nature to do the will of the worshippers.

From such humble beginnings came the exalted ethical teachings of Zarathustra, of Lao-tse, of Buddha, of Jesus. These bodies of doctrine did not appear miraculously like Melchisadek, without ancestry, but came about as the ultimate fruition of the perpetual striving of the genus *Homo* to pierce the veil of the temple of nature—a striving that is firmly rooted in the fetishism and animism of the palaeolithic cave man.

The teachings of such intellectual leaders constitute ethics, but the systems of belief that accumulate about the memory of them constitute theologies, and it is with theologies that this author is chiefly concerned. He traces the evolution of the various components of contemporary Christian thought from Sumerian and later aboriginal sources to the present.

The author is particularly happy in his treatment of the cultural aspects of warfare. In a very timely discussion he points out that it is to the defeated and conquered Athenians, and not to the victorious Spartans, that everything good in Greek civilization is due. The militarism that won the war for Sparta also precluded that state from making any substantial contribution to Greek culture, and to the pacifism that brought about its defeat on the field of battle Athens owes its immortality. The lesson seems to be that pacifism is the most practical course for a people who wish to leave an indelible

imprint on the civilization of coming ages.

A peculiar feature of the work is a consistent tendency to assign pre-Christian era events a date one year later than that commonly accepted by authorities. Apparently this is an attempt to supplant the illogical chronology to which historians are addicted by the more exact system used by astronomers. The contiguity of the years one B.C. and one A.D. in historical chronology is due to the accident that when Dionysius Exiguus devised the method of dating events from the Nativity there was as yet no zero in the European mathematical scheme. The attempt to restore the zero year as astronomers have done is altogether laudable, and the author deserves congratulations for his courage.

The index covers only ten pages, which is quite inadequate for the wealth of material between the covers of this book, which is exceedingly well written and highly stimulating.



CLASSIFIED INDEX TO THE PUBLICATIONS
OF THE AMERICAN PHILOSOPHICAL SOCIETY,
1769-1940.

American Philosophical Society, Philadelphia. Free. 8½ x 5½; v + 173;
1940 (paper).

During the long career of the American Philosophical Society (in another two years it will celebrate its two hundredth anniversary) many important papers and communications reporting advances in science and in thought in America have been reported at its meetings. In its very early years the Society issued no printed records but in 1769 *The Transactions*, now the oldest scientific journal in America with a continuous history, appeared. The first six volumes (old series) were in small quarto format. In 1818 a new series, the present large quarto format, was started and to date, 31 volumes have been published. *The Proceedings*, containing original papers read before the society and others accepted for publication, also abstracts, and verbal communications and letters on scientific and learned subjects (of special interest to research students

and historians), first made its appearance in 1838. It was not until 1935 that the *Memoirs*, consisting of monographs of book length, each constituting a separate volume of the series, was started. Other publications are the *Year Book* and *Miscellaneous Publications*. In the present list, papers and books are classified under fifty headings, ranging through all branches of the sciences, and literature, philosophy, languages, politics, biography, and exploration. On a rough estimation, we place the number of items at about 3500. Many of the early papers are out of print, but the Library maintains a Photoduplication Service and for a nominal sum will furnish copies of out-of-print articles and manuscript material.

A price list follows the classified list—there is no attempt to push prices upward—and an index of author's names concludes the catalogue. Anyone desiring to enrich his library would do well to study this catalogue with care. It will yield many desired items.



FROM BEAST-MACHINE TO MAN-MACHINE.
Animal Soul in French Letters from Descartes to La Mettrie.

By Leonora C. Rosenfield. Oxford University Press, New York. \$3.50. 8½ x 5½; xxviii + 353; 1941.

This is the history of a strange idea, held but little nowadays—that the animal body is a mechanism in the strict sense. Not merely that the motions of the body take place in accordance with the laws of mechanics, for that is quite obvious, but that consciousness itself is only a function of material organization and must not be postulated except when verified by experience. Even the construction in the remote future of robots actuated magnetically to do all that a man can do is not an impossibility. The doctrine seems to have originated with Descartes, who went through a stage of materialistic thinking in his youth. Later when the great French philosopher admitted the existence of the human soul, the doctrine of the kinship of man to the rest of the animal kingdom had become repugnant to the ecclesiasts, and Descartes found it ex-

pedient to continue to regard the sub-human animals as automata, without power to feel or to think.

La Mettrie, on the other hand, was a medical man, capable of appreciating man's systematic position among the animals. But being under no obligation to the ecclesiasts he accomplished his synthesis of the animal kingdom not by recognizing the animal soul but by denying the human soul. It is true that he was not always consistent—what philosopher is?

The author presents a scholarly analysis of the doctrines of these two writers and a host of others between them, and has provided an extensive documentation and an exhaustive index.



THE SOCIAL ROLE OF THE MAN OF KNOWLEDGE.

By Florian Znaniecki. Columbia University Press, New York. \$2.50. 7½ x 5½; 212; 1940.

How has the seeker after knowledge, the scientist or, more precisely, the savant attained his present position in our society? This is the question that Znaniecki attempts to answer in this monograph which summarily describes the processes of social interactions involving the cultivator of knowledge. The author apparently views these processes in the form of a gradual evolution of individual ideation and of group consciousness. At first the individual technical skill and interest is dedicated to the narrow field of immediate practical needs, then the individual advances beyond the needs or expectations of the social group. He becomes the technological inventor. Similarly with respect to so-called spiritual needs the sage emerges into the scholar and later the "scientific explorer." While the technologist and the sage acquired elevated social standing because they coupled knowledge with authority, "scientists came to be socially accepted because and in so far as they specialized in cultivating a kind of knowledge which men of action regarded as useful for practical purposes." Scholars have assumed their social position because they have

convinced others and are themselves convinced that knowledge gives power "because and only because it is pure theory, an objective system of truths, and man must know reality truly in order to control it effectively." The author has obviously only begun to probe the question, nevertheless this exposition will interest all scholars and scientists and is a contribution to a sociology of knowledge.



TEMPERATURE MEASUREMENT.

By Robert L. Weber. *Edwards Brothers, Inc., Ann Arbor, Michigan.* \$2.50. 10 $\frac{1}{2}$ x 8; x + 171 + [6]; 1941 (paper).

"It is the purpose of this book to outline an experimental study of the methods of temperature measurement with the theoretical principles necessary for their appreciation, intelligent use and extension."

The principles involved are presented in Part I. This includes concise discussions of the theoretical, and descriptions of the practical, methods used in expansion and resistance thermometry, thermoelectric and radiation pyrometry, recording of temperatures, automatic temperature control, colorimetry, and measurement of extreme temperatures. Further theoretical sections deal with thermal analysis and elementary thermodynamics. In addition to a list of problems designed to familiarize the student with this highly technical subject, the second part of the book is devoted entirely to experiments illustrating the principles previously described. An extensive appendix contains tables of physical constants, temperature conversion, and thermocouple characteristics for various metals.

Besides being a well organized and useful text, this book should find widespread acceptance in many fields of scientific and industrial research.



THE MICROSCOPE.

By R. M. Allen. *D. Van Nostrand Company, New York.* \$3.00. 9 x 5 $\frac{1}{2}$; viii + 286; 1940.

From its early use by amateur enthusiasts,

the microscope has steadily increased in importance until at present it is an indispensable tool not only in the various phases of biology, but also in other sciences and industry. All too few people who must use this instrument fully understand its principles, thus impairing the quality of their work. The author has outlined these principles and methods of handling the microscope in the clearest possible terms, so that even those without training in optical science will become better acquainted with the microscope by reading this book. A chapter on the history of the microscope is followed by discussions on optical principles, descriptions of lenses and various mechanical devices of modern microscopes, and instructions in the use of the microscope, including illumination and techniques of preparing material for microscopic study.



INTRODUCTION TO LOGIC and to the Methodology of Deductive Sciences. Enlarged and Revised Edition.

By Alfred Tarski. Translated by Olaf Helmer. *Oxford University Press, New York.* \$2.75. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; xviii + 239; 1941.

The Greeks were the great logicians of antiquity but they were not mathematicians, and consequently their logic lacked the precision and exactitude demanded by a world of non-Euclidean geometries and relativity physics.

The present work is intended to supply this lack, and is based on mathematical axioms and expressed in mathematical formulae. It will doubtless succeed eventually in supplanting the classical logic of the trivium. It is intended for use as a text book, and is well provided with exercises. Also it has a bibliography and an index, both of which are quite comprehensive.



HOW TO BUILD AND EQUIP A MODERN DARKROOM.

By *Nestor Barrett and Ralph Wyckoff*.
Camera Craft Publishing Company, San Francisco. \$2.00. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; 133; 1940. Many amateur photographers spend large sums of money on equipment for taking good pictures and then produce only mediocre work because of an inadequate darkroom. Detailed descriptions are given in this book for building a good photographic laboratory which will be

adaptable to basement, attic, or apartment. Prices are included so that the individual may plan within his budget. Surfacing, ventilation, lighting, plumbing, and accessories are all thoroughly discussed and diagrammed. A supplementary chapter describes a home motion-picture auditorium for advanced enthusiasts. Many time- and money-saving ideas are incorporated in these pages.



THE QUARTERLY REVIEW *of* BIOLOGY



ORGANIC POLARITY SOME ECOLOGICAL AND PHYSIOLOGICAL ASPECTS

By R. S. WIMPENNY

INTRODUCTION

THE polarity with which I propose chiefly to deal, is that interesting and quite well-known sequence of communities, species, forms, and physiological groups that are found in a uniform medium as it stretches from the equator towards either pole.

Johnstone (57) among others, has already stated the matter in part. Considering the work of the German planktologists, Hensen and his collaborators, and the observations of other naturalists, he concludes that the warmer waters of the world produce less abundant but perhaps more varied plankton and that the algal flora and benthic and nektic life is poorer in warmer than in colder seas. This difference is in the opposite sense to the distribution of terrestrial life, which is densest in the tropics and diminishes towards either pole, apparently in direct relation to the intensity of sunshine and temperature. The chemical and physical aspects of this question have been raised by Sir John Murray (78) who points out that there are in the sea three surface zones of different character. The first is the cir-

cumtropical zone, where there is a high temperature throughout the year and an annual range not exceeding 10°F. Here is the area in which live all those organisms which form massive skeletons of calcium carbonate laid down chiefly as aragonite; here also metabolic changes take place very rapidly and pelagic larvae are abundant. Between the circumtropical and circumpolar zones are two zones in which the temperature range may be as high as 45°F. causing a great destruction of animal life with a consequent deposition at the bottom of the ocean of phosphatic and glauconitic nodules. In the circumpolar zones there is a low temperature with an annual range not exceeding 10°F. and in which such little calcium carbonate as is found in living organisms occurs in the form of calcite. The metabolic changes take place slowly and pelagic larvae are almost absent. Murray goes on to suggest that in a warm zone an organism may pass through its whole life-cycle in a few hours, days or weeks, whereas a similar organism in polar waters may take years to pass through a similar life-cycle. Further-

more, he points out that the optimum temperature for most vital enzymes is blood heat and that none is known to have an optimum temperature as low as that in which polar invertebrates must live.

In his recently published work *Tiergeographie des Meeres*, Ekman, (29) who is more particularly concerned with the systematic aspect of animal distribution, recognizes in his consideration of "bipolarity", a bipolarity of parallel phenomena. The bipolarity considered by Ekman is chiefly one of related forms that have become discontinuously distributed, but the bipolarity of parallel phenomena is characterized by ecological differences such as greater numbers of individuals, the greater size of these individuals, thinner shells and greater brood-care towards the poles. It is also shown by the circumstances that a family or genus inhabiting cold or temperate areas has a greater number of species than is the case in tropical seas, and finally by the occurrence of species living in the seas of lower latitudes and from each of which may be derived a different species or variety which is found towards either pole. This latter sort of bipolarity is called the bipolarity of taxonomic parallel development (*Bipolare taxonomische Parallelentwicklung*).

Discussing the ecological differences in another part of the book, Ekman accepts as a fundamental principle Thienemann's generalization that the more an environment departs from the normal and the more specialized and extreme it becomes, the poorer it becomes in species and the richer in numbers. The implication of this statement is that the colder seas present an extreme and specialized environment compared with a normal and optimum area in the tropics. This definition of the two areas is the one which I am not disposed to accept for reasons which will appear later.

My purpose in the argument that follows is to develop some of the conclusions and speculations just mentioned. Briefly I conclude that the gradient of radiant energy in an otherwise nearly uniform medium like the sea, sets up a gradient of assimilation in living things. This results in organisms living more quickly, showing a greater variety of form, often accumulating different end-products, occurring in more complex communities and being present in less total mass, area for area, in the tropics. At any place on this gradient, differences of season, passive convection and vertical distribution may produce conditions similar to another part of the gradient.

I have also attempted to relate the ratio of the sexes in particular species of organisms to the polarity that has just been defined. Assuming the metabolic theory of Geddes and Thomson (35) we should expect to find the females of any species more successful where the food conditions are best, and the males where food conditions are unfavorable. Also, other things being equal, we should expect to find the quicker metabolism of the males favoring their relative increase at the hotter end of the range of any one species. That these relations do actually occur is, I think, shown by my evidence. The amount of observation available concerning the size, number, physiology, and distribution of living things that might serve my purpose is necessarily enormous.

The generalizations I am about to make are therefore drawn from instances I have come across in the course of other work, general reading, and also occasionally from my own investigations. Many of these instances are quite well known, but I do not think they have been presented in such a way before. As the land areas present an environment of extreme complexity, most of my examples are taken

from the sea, where conditions are more uniform and effects are likely to be more simple. Nevertheless, I have not hesitated to deal with terrestrial organisms in certain parts of my argument, particularly in the section on sex-ratios.

Finally, I cannot pass from this introduction of the factors I am about to deal with in respect of the distribution of organisms on the earth's surface without mentioning the qualitative parallelism they exhibit to the physiological gradients already established in individual organisms. Metabolic gradients are well known as the result of the work of the embryologists who have shown that there is a gradient both in activity and in chemical composition between the animal and vegetable pole in the eggs of certain vertebrates. Similar gradients in adult organisms have also been shown. The considerable data available in this field has been well marshalled by Child (19) who has been responsible for many of the important experiments demonstrating axial gradients. When discussing metabolic gradients in eggs, the term "polarity" is often used and though the term "bipolarity" denotes the faunistic resemblances of the seas at two poles in contrast to the conditions of things at the tropics, I have retained the more simple word "polarity" as the title of this paper, thinking it better to stress the essential unity of the phenomena discussed here with those of a wider field.

AN ASSIMILATION GRADIENT

The work of Hensen (46), Lohmann (68), Hentschel (47), and others has shown that there is a general increase of plankton organisms as one moves from low to high latitudes in the ocean. This increase applies to both plant and animal elements. For the North Atlantic it has been usefully expressed by Harvy (45) in

the table adopted from Lohmann's work (Table 1), showing the phytoplankton organisms per litre between the surface and 400 metres.

The diagrams reproduced in Fig. 1 are from Hentschel's work and show the same conditions rather more fully for the microplankton and Metazoa of the South Atlantic. The conditions necessary for the growth and reproduction of plankton algae upon which the rest of the plankton depends, are a nutrient medium containing a sufficient inorganic food supply and the radiant energy of the sun. The sea forms such a medium, but Atkins (6) and Harvy (43) have shown that the growth of algae

TABLE 1
Frequency of phytoplankton organisms in different latitudes

LATITUDE	40°- 50°N.	30°- 40°N.	20°- 30°N.	10°- 20°N.	10° N.
As found in	May 6,000	June 2,000	June 600	500	600
Surmized mean for whole year	3,000	1,000	600	500	600

may utilize completely now the available supply of phosphates and now that of nitrates. Both these salts are necessary for the elaboration of living protoplasm and their absence sets a limit to further growth. Other salts or elements occurring in sea water in minute concentrations may also be necessary for the growth of algae. For instance, recent investigations made by Gran (39) have stressed the importance of iron compounds. Nevertheless, the availability of phosphates and nitrates broadly fits the observed facts of algal distribution.

Now the distribution of these two important ultimate foodstuffs, phosphate and nitrate, shows that they occur in relatively large quantities in the deeper water of the

great oceans, both in the tropics and the polar regions. But at the surface of the oceans, and in the shallower water near the coast, or submarine banks, there is no such uniform abundance. In high latitudes in the winter and spring, the amounts of phosphate and nitrate in the surface water of the oceans may be far greater than those found in the warmer parts. This phosphate and nitrate is subsequently almost entirely used up by

An attempt to explain the distribution of ultimate foodstuffs in the surface waters of the great oceans may be helped by a consideration of this figure, for though the nitrate values have not been plotted their behavior is similar. In warmer seas the nutrient salts mentioned are used up as soon as they become available in the upper water layers. This is on account of the powerful and abundant solar radiation available for photometabolism

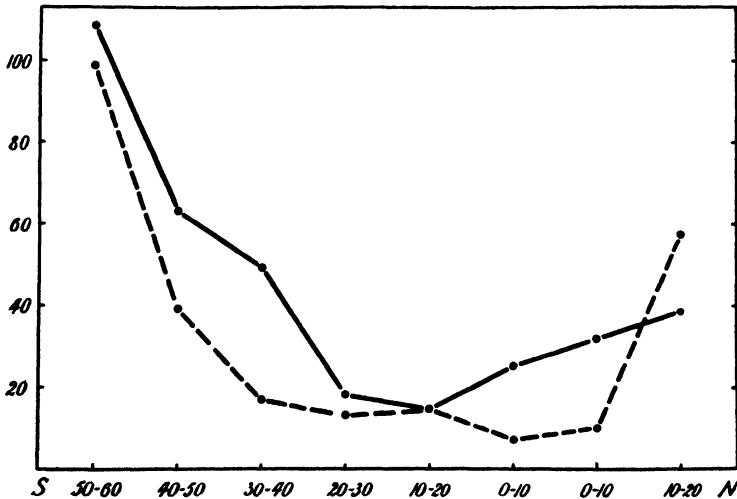


FIG. 1. THE AVERAGE CONTENT PER LITRE AT 0 AND 50 M. FOR NANNOPLANKTON (BROKEN LINE) AND PER FOUR LITRES FOR METAZOA (CONTINUOUS LINE) GROUPED ON THE ABSCISSA AT 10° LATITUDE INTERVALS FOR THE ATLANTIC

The figures on the ordinate represent 1000s for the nannoplankton and units for the metazoa (After Hentschel)

enormous outbursts of algal growth. In South Polar seas, however, Deacon (25) has recently shown that the very great amounts of these nutrient salts present at the surface are not exhausted in this way even at the times of vigorous algal growth.

In Fig. 2, I have constructed a composite chart showing the milligrammes of phosphate at different depths in the Atlantic between the North and South Poles and based upon the results of Krebs and Verjinskaya (61), Atkins (7), Thomsen (116), and Deacon (25).

throughout the year. But in boreal seas, solar radiation is less intense and insufficient for any considerable photometabolism in the winter. During this period the surface water, which has become sharply separated from the deep layers by its higher temperature, cools, and becomes heavier and therefore sinks. This causes vertical mixing and results in the bringing of phosphate- and nitrate-rich water to the surface. On the arrival of the long light days the conditions are fulfilled for the enormous abundance of algal growth mentioned above. The

shortening summers and more rigorous winters of increasing latitudes give not only a much deeper exchange between the surface and the deeper waters, but this exchange continues longer and longer into the time of algal reproduction. This difference in vertical mixing, fundamentally a temperature effect, is no doubt the principal cause of the observed increasing abundance of oceanic microplankton with latitude.

There is, however, another factor which would produce a greater mass of microplankton plants and animals in higher

serratus, where a decrease in temperature was found to lower the rate of respiration to a greater extent than the rate of photosynthesis. Whether this is generally the case or not, it seems clear that the animal plankton would be able to live more economically on the same amount of algae.

There are two other factors that may have favorable effects on the production of algae in higher latitudes; one is the effect of polymerized water due to the melting of ice, and the other is the greater solubility of CO_2 in the colder water.

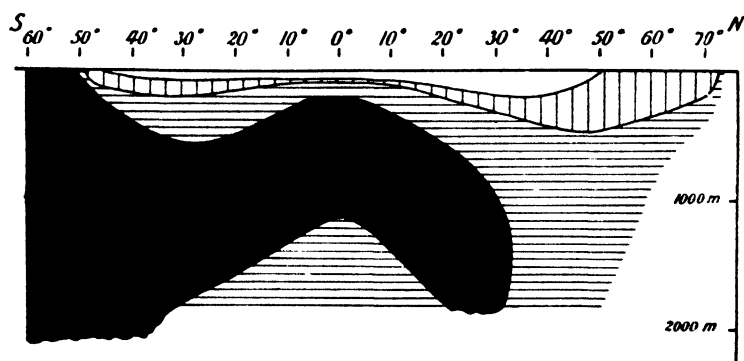


FIG. 2. SCHEMATIC SECTION OF THE ATLANTIC SHOWING THE DISTRIBUTION OF P_2O_5 AT DIFFERENT LATITUDES AND DEPTHS

The contours are at 30, 50, and 100 mgms. per cubic metre

latitudes. This is the direct effect of temperature. According to the Van't Hoff generalization, a rise of 10 degrees centigrade brings about an increase of approximately double the rate of vital metabolism, when this change is applied within the range the species is capable of tolerating. This would mean that organisms in higher latitudes would be able to conserve their same mass with less energy. In the case of the algal producers, this might be offset by a correspondingly lower rate of production of the food from which the energy would be obtained. According to the work of Kniep (59) this is not the case in the brown alga, *Fucus*

There is not yet, however, sufficient data bearing on these two effects to permit a fruitful discussion.

In addition to the conditions just mentioned, there are two ways in which solar radiation might be expected to operate more favorably for plant reproduction in the tropics. Firstly, the annual solar radiation is greater in the tropics (though that of a long polar summer's day is greater than that of a tropical 12-hour day) and light penetrates further into the sea, shortening the distance that regenerated phosphates and nitrates would have to move upward. Secondly, the high surface temperatures of tropical seas, will

give rise to much evaporation, causing a cooling and a mixing of the superficial layers throughout the year. Nevertheless, the factors working in the opposite direction discussed at the beginning of this section obviously outweigh these two particular effects of solar radiation.

There must be mentioned here also the fact that the regularity of this production gradient is often upset by upwellings of

effects takes place off the coast of California.

This section may be concluded by saying that there is a general increase in microplankton abundance with increasing latitude in the great oceans, and that this is fundamentally an increase of the photosynthetic plants and their more successful assimilation. The cause of this gradient of assimilation is a gradient of solar

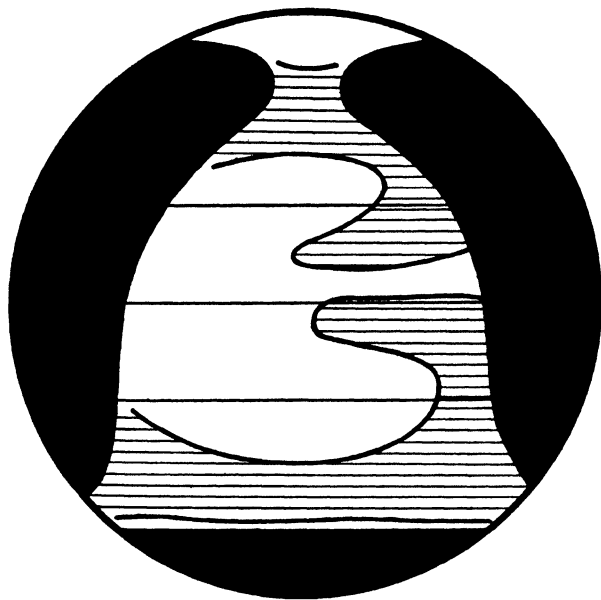


FIG. 3. GENERALIZED PICTURE OF THE DISTRIBUTION OF PLANKTON IN ANY OCEAN
The plankton-rich parts are indicated by parallel lines (After Hentschel)

salts due to currents, tides and turbulence in the neighborhood of submarine slopes and the incursion of river water near the coast. This results in favorable conditions for plant growth and a profuse flowering.

An instance of upwelling occurs near the equator, and the effect on phytoplankton abundance is shown in Table 1, where it will be noticed that the number of organisms between 0-10 degrees N. is greater than that between 10-20 degrees N. (Fig. 3). Another case of upwelling having similar

radiation. This acts indirectly by establishing a gradient of thoroughness in the mixing of food—rich deep water with the exhausted upper layer—and directly but perhaps not so importantly by increasing the rate of living in the warmer waters, without the presence of the means for a corresponding assimilation.

VITAL VELOCITIES

The building up of living matter takes place in two ways. In one, the substances produced by living things or the living

things themselves are utilized. In the other, inorganic substances are absorbed and united within the body of the organism to make organic matter with which to build up the living protoplasm. Plants utilize this method and animals the former. In the marine plankton the plant type of life is sometimes called "producer" and the animal type "consumer" plankton.

It is clear that the relation of all living things to that part of the inorganic environment which is essential to assimilation will be governed by the plants. Another way of presenting the matter is to consider the position of plants among all living things as a group that stands nearer the building up or anabolic side of the great vital process which is constantly building itself up and breaking itself down. On the other hand, animals, starting with the assimilation of substances that are the end results of the plants' activities, must be considered as relatively nearer the break-down or catabolic side of the life process as a whole.

While the energy used by the plant in the course of assimilation is very great, the result is an organism that achieves growth in bulk, but is usually devoid of kinetic activity. The animal, however, not only grows, but frequently utilizes the energy obtained from its organic food in movement. The rate of living is relatively increased, and the break-down processes take place at a greater rate than in plants. In most animals indeed, there are special organs of excretion to deal with the rapidly formed and copious end-products. Notwithstanding this general division of animal and plant, or "producer" and "consumer", types of life there are certain organisms shortly to be mentioned that behave on the whole as producers, but exhibit certain features of the consumer class.

In the light of what has just been said

let us consider the distribution of some of the largest and most important groups of organisms in the great oceans. To the plants belong a great community, the algae, on whose photosynthesis of inorganic matter into organic, the greater part of the rest of the life in the sea depends. Of the algae the most important and widespread group is that of the diatoms, but it is towards the poles that this group has its greatest absolute and relative abundance. In lower latitudes diatoms are replaced in importance by the calcareous and flagellated Coccolithophoridae and the blue-green genus *Trichodesmium* as the dominant algae. In the hottest waters the dominant producer community is that of the peridinians. The peridinians are unicellular organisms capable of photosynthesis but protected by a wall of cellulose plates and not by a siliceous one as is the case in diatoms. They are also provided with powerful flagellae seated in special grooves on the surface of the body. These flagellae are organs of movement and like those of the Coccolithophorides already mentioned endow their possessors with the power of movement. As groups, therefore, the peridinians and Coccolithophoridae resemble the animals in that they are kinetic, and so must be regarded as living more quickly than the diatoms of the plankton. The sequence of communities just discussed is shown in Fig. 4 which is taken from Hentschel's (47) plankton survey on the "Meteor's" expedition to the South Atlantic and which together with Figs. 1 and 3 he has kindly allowed me to reproduce. In parts of the world where there are marked seasonal changes the spatial sequence of communities that have already been mentioned is essentially repeated in time. Discussing the results of the periodic plankton cruises of the International Investigations in Northwest Europe, Gran (38) says

It is characteristic for the yearly period of the plankton for the whole of our area, that the development after the winter rest commences everywhere with a strong flowering of diatoms—succeeded by the next stage in the development, the *Ceratium* (peridinium) plankton which with comparatively unimportant modifications is usually prevalent throughout the summer.

experience of all planktologists working in temperate latitudes.

Turning to fresh water it is significant for the present argument to note that West (124) says of the peridinians that they occur in Britain only in the summer, but are found perennially further south. In

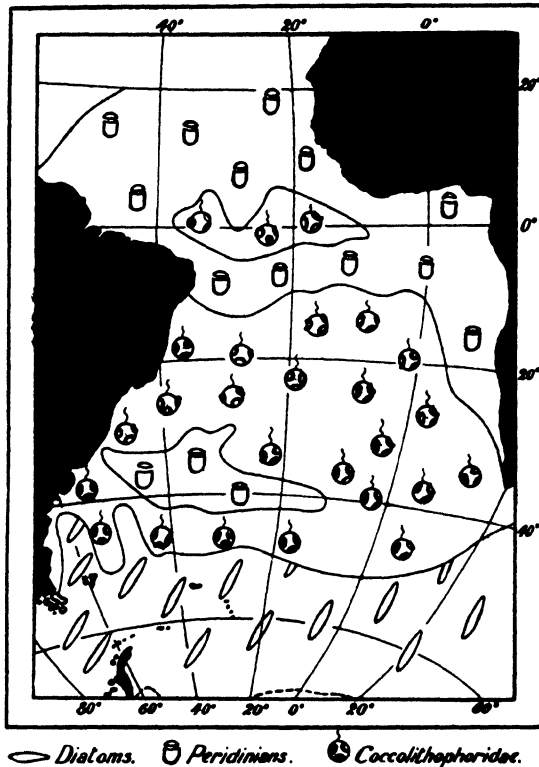


FIG. 4. CHARACTERISTIC NANNOPLANKTON ORGANISMS IN DIFFERENT ZONES OF THE ATLANTIC (After Hentschel)

In addition it may be said that the larger zooplankton organisms behave like the peridinians in that they follow the diatoms. There is usually a secondary outburst of diatoms in the autumn, but they are often of different species, and later I shall suggest that there are physiological differences. The annual sequence described here has been the general

fresh-water lakes vast masses of blue-green algae may occur in the still hot water of high summer long after the spring diatom outburst. Some of these species possess a peculiar power of movement, the nature of which is not yet properly understood. Blue-green algae are further notable in that some of their species are found at the highest temperature known

to be tolerated by living organisms, when they occur in hot springs at as much as 78°C.¹ The seasonal occurrence of blue-green algae in fresh water recalls the masses of *Trichodesmium* found in the warmer parts of the ocean.

I began this section by defining animals and plants as organisms of different types of assimilation, the animal type consuming the results of the plant type's production and living at a greater rate. I also show that certain important groups of producer plankton of tropical and temperate seas were absent from the neighborhood of the poles and that these groups bore indications of a quicker and more animal type of metabolism. Thus the hotter regions, as we might expect, favor the more catabolic types of metabolism among the producers by a general increase of vital velocities. At first sight this acceleration of vital velocities also might be thought to favor the animal and consumer plankton in contrast to the producers. It must be remembered, however, that if, as is very broadly true, the vital rate of wastage is doubled for 10°C. rise in temperature, the consumer plankton would need twice the amount of producer food in order to maintain its original bulk. This means that, with the same amount of producer food at the two temperatures, the proportion of consumers supported by producers at the higher temperature would be halved. The proportion of consumers to producers should, therefore, fall as the temperature increases. A further inference from this thesis is that if the amount of producer plankton were the same at the poles and the equator, the total plankton at the equator would be less as a direct result of the gradient of solar radiation causing a less proportion of consumer plankton at its higher end. Actually as we saw in the preceding section the

producer plankton is itself less at the equator than at higher latitudes.

The general relations between producer and consumer plankton expected on theoretical grounds appears to occur in nature, for according to Lohmann (68) the mean ratio of Protophyta, Protozoa and Metazoa in the centrifuge plankton of his "cool areas" was 741:73:1, and for tropical areas 458:24:1.

The matter can be summarized by saying that in the microplankton there is an absolute and a relative preponderance of kinetic compared with static organisms as we approach the equator, though Lohmann's careful work shows that the photosynthetic species are supporting relatively less consumers.

FAT AND CALCIUM CARBONATE

Fat

Brandt (16) and Delff (27) for marine plankton, and Birge and Juday (14) for that of fresh-water lakes, have shown that relatively more fat than carbohydrate was laid up by diatoms as compared with peridinians. For other motile microplankton organisms, Delff (27) gives less than 2 per cent of fat and over 60 per cent of carbohydrates for a sample of the radiolarian *Collozoum inerme* from the Mediterranean and I have found ether-soluble matter values of 2.7 per cent and 3.3 per cent of the dry weight for the flagellates *Phaeocystis* sp. and *Noctiluca miliaris*—lower values than those shortly to be given for diatoms from the same area.

The low fat and higher carbohydrate values indicated by these results for motile organisms are significant, when we remember that physiologists have shown that only a carbohydrate can be readily utilized for muscular movement. The relatively greater amount of this easily mobilized food reserve in the more kinetic

organisms seems, therefore, an inevitable physiological side of their motility and their generally higher position on the temperature gradient.

As showing an increased percentage of fat at a lower temperature, it is interesting to compare the 2.07 per cent of dry weight for the diatom *Aulodiscus kistoni* at the time of its maximum in May on Copalis Beach, Washington, and at a temperature of 13°–16°C. (11) with my comparable and hitherto unpublished estimates of 28 per cent–48 per cent for *Coscinodiscus concinnus* during its maximum in May, 1933, when it was found on the Dogger

Ministry of Agriculture and Fisheries research ship "George Bligh."

A number of similar estimates for Hensen net hauls made in June and October, 1932–1934, in the western North Sea, and consisting mainly of zooplankton have been correlated with the corresponding bottom temperatures in the list below:

Year	Month	Number of Stations	r
1932.....	June	30	−0.76
	October	27	−0.42
1933.....	June	35	−0.67
	October	27	−0.45
1934.....	June	32	−0.63
	October	26	−0.435

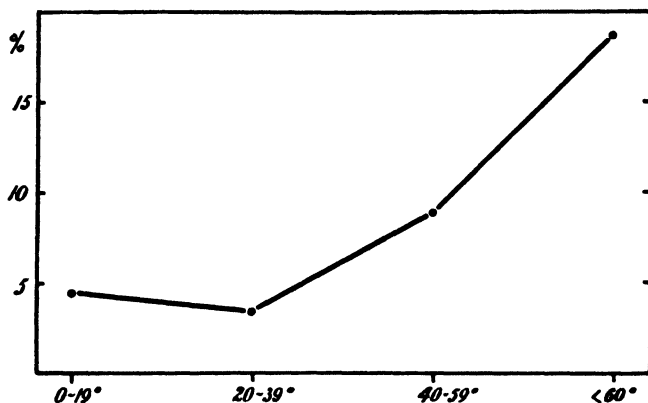


FIG. 5. THE PERCENTAGE OF FAT IN THE DRIED COARSE NET PLANKTON COLLECTED NEAR THE SURFACE AT SEVERAL STATIONS AND EXPRESSED AS THE MEANS OF FOUR ZONES OF LATITUDE

Bank at a temperature of 6.5°C.–10°C. For a wider latitude range, I have determined a series of 17 fat percentages for coarse net plankton samples which have been averaged in 20° groups in Fig. 5 against latitude, with which the fat values show a tendency to correspond. The material was almost entirely zooplankton collected in the upper water layers of the North and South Atlantic and the Indian Ocean. I am indebted to the late Mr. J. O. Borley and Dr. Stanley Kemp for the "Discovery" collections and to Mr. M. Graham for those made by the

The highest fat values always came from the northern part of the area where the bottom temperatures were lowest, and the negative correlation was always greater in June than in October.

A qualitative difference in fat with latitude and temperature has been indicated for land plants by Ivanoff (56) while Leathes and Raper (63) suggest that fats generally are of a lower melting point at the lower temperatures of high latitudes.

Seasonal variations of fats and carbohydrates for mixed Hensen net catches have been given by Brandt (16), and to

these I add, in Table 2, the monthly mean percentage fat-content of six routine stations which I have regularly investigated in an area between Flamborough Head and the Dogger Bank from 1932 to 1936. The values are also shown as a graph in Fig. 6.

These results show fat production to have reached its highest in late spring and early summer, at a time somewhat after the temperature minimum. Values

cooler water of spring. The percentage of ether-soluble matter for two of these species taken in similar positions in the same year, but in the spring and autumn respectively, are as follows:

<i>Coscinodiscus concinnus</i>	18.8
<i>Rhizosolenia styliformis</i>	4.1

For *Biddulphia sinensis* the figure is almost the same as for *Rhizosolenia styliformis*.

TABLE 2
Seasonal variation in plankton of fats and carbohydrates

No. of stations dealt with	16	17	22	20	22	30	30	23	30	29	30	21
Percent ether soluble matter to dry weight at 80°C.	11.7	7.0	9.2	13.0	18.0	15.1	15.2	10.9	12.1	11.1	12.1	14.4
Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII

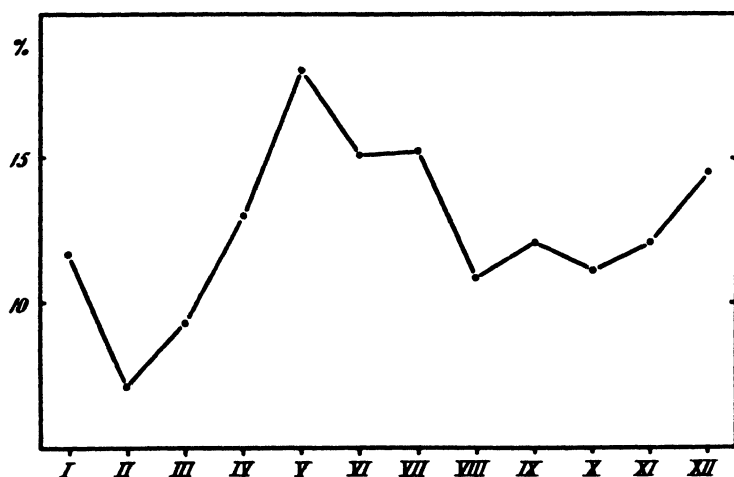


FIG. 6. SEASONAL VARIATION IN THE PERCENTAGE OF FAT TO DRY WEIGHT FOR HENSEN NET PLANKTON CAUGHT NEAR FLAMBOROUGH HEAD

were comparatively low in the late summer and autumn when peridinians predominate.

There is also an interesting difference between species of diatoms characterizing different seasons. In the North Sea, *Rhizosolenia styliformis* and *Biddulphia sinensis* are autumn forms, while *Coscinodiscus concinnus* occurs more often in the

The seasonal differences in the fat-content of diatoms and of mixed Hensen net catches are accompanied not only by differences in radiation, but, according to the work of Atkins (6) and Harvey (43) by parallel differences in the amounts of nutrient salts available for algal reproduction. The work of Graham (40) also suggests that the same parallelism may

occur in the regional variation of the ether-soluble figure for the North Sea area which I have already mentioned. These complications appear to be absent from investigations made by Ahmad (2). Under controlled laboratory conditions this worker found more fat in the colder seasons for cultures of *Nitzschia closterium* grown in modified Miquel's solution.

that lower temperatures facilitate the formation of fat.

Calcium carbonate

One of the most important end-products is calcium carbonate, responsible not only for the relatively considerable skeletons of the Coccolithophoridae, already mentioned as characteristic of the plankton

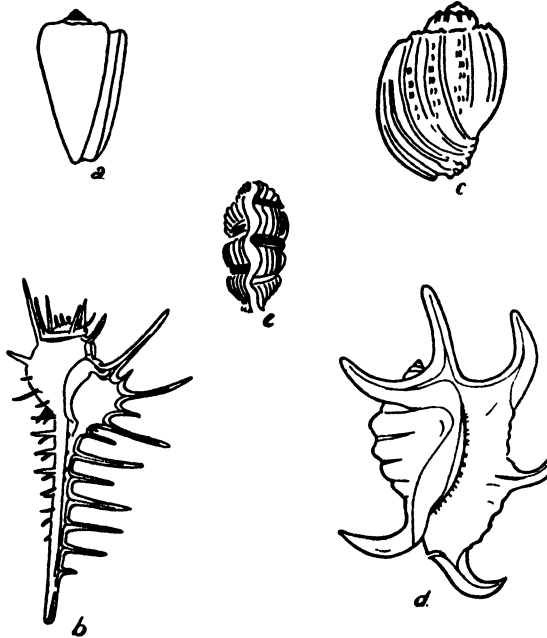


FIG. 7. (a) *CONUS MARMOREUS*: (b) *MUREX ACANTHOSTEPHUS*: (c) *HARPA VENTRICOSA*: (d) *PTEROCEROS RUGOSUM*: (e) *TRIDACNA SCAPHA*

Considering pelagic Crustacea, the case of *Calanus finmarchicus* is worthy of note. According to Nicholls (81) this species spends the winter as a stage V copepodite, and it is in this stage that it is fattest, although it must be said that the highest values actually found for this stage were recorded in the summer. Experiments carried out by Geoffrey Smith (111) are of further interest in this connection, his work on the *Cladocera* appearing to show

algae in the warmer parts of the ocean, but also for those of an important group of protozoa, the Foraminifera, and among molluscs, the Pteropoda.

Along the littoral zone between the poles and the equator, the big brown algae are replaced by smaller red forms, among which the species that calcify become more important as the temperature increases, until that massive calcification of certain species known as nullipore

"coral" appears in the sub-tropical zone. In the tropics these are succeeded by the limy masses of the true coral which often make up the entire shore. In this latter

ples of these are the species of the genera *Tridacna*, *Spondylus*, *Murex*, *Harpa*, *Conus*, *Pterocera*, etc. (Fig. 7). Among teleostean fishes, the distribution of the Acanthop-

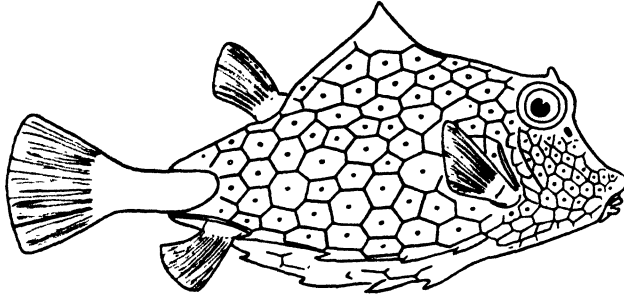


FIG. 8. *OSTRACION TURRITUS*
(From Day)

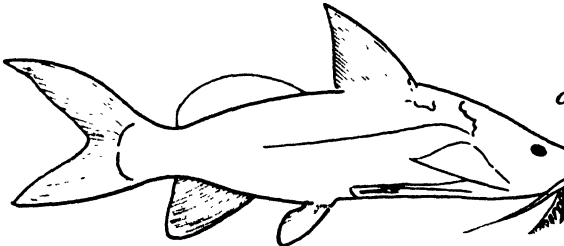
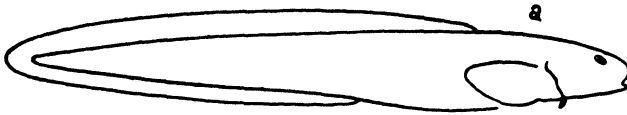


FIG. 9. (a) *LYCODES FRIGIDUS* (ARCTIC DEEP WATER): (b) *PTEROPHYRNE HISTRIO* (SARGASSO SEA): (c) *SYNODONTIS SCHALL* (NILE)

habitat are also found a variety of species belonging to the Gastropoda and Lamelibranchiata characterized by the great size and thickness of their shells. Exam-

terygae—a group recognized by earlier systematists as characterized by bony fin-rays—is mainly tropical and warm temperate. Species inhabiting the tropical

coral coasts are often very heavily ossified, culminating perhaps in forms like those of the family Ostracionidae, where the body is a completely rigid armored box (Fig. 8). Outside the Acanthopterygae, the Siluridae, a family whose fresh-water species are found most abundantly in the warmer parts of the world, show species with heavily ossified heads and pectoral spines such as occur in the genera *Synodontis* and *Schilbe* (Fig. 9).

In the deep sea, Gorgonid, Isid and "star" corals (*Oculina* and *Amphibelia*) present in the Atlantic are absent from adjacent deep parts of the cooler Norwegian Sea (5). In the cool depths of the ocean there is also a general lack of ossification in fishes at all latitudes.

Finally, it may be pointed out that increased calcification of the human skull at lower latitudes is shown when the tropical Negro is compared with that of the European. This matter is the subject of interesting comment by Herodotus (49), when describing the battlefield of Pelusium where Egyptian and Persian dead lay side by side.

The relation of calcium to the formation of fat and calcium carbonate

Work done by Pearsall (91) on diatoms and by Sherman and Quin (107) on rats has suggested a relation between fat and calcium. A similar correspondence also appears on consideration of Brandt's (16) analyses of copepods and some of my unpublished results for diatoms:

	Per cent fat	Per cent CaO
North Sea Stn. 7 (Copepoda)	19.23	0.43
North Sea Stn. 4 (Copepoda)	4.59	0.16
Vg.H. Stn. R (<i>Rhizosolenia</i> <i>styliformis</i>)	4.1	0.91
Vg.A. Stn. 31 (<i>Coccinodiscus</i> <i>concinus</i>)	18.8	3.38

Clowes (20) considers that the presence of a preponderance of calcium ions at a cell

surface favors the formation of fat by throwing the oil-water emulsion at this surface into an oily phase due to the formation of an insoluble soap. Potassium and sodium, however, form soluble soaps.

On the other hand, calcium may be removed from a solution (where it is available to facilitate the formation of fats) by its precipitation as insoluble calcium carbonate. According to Sir John Murray (79) this may take place in two ways. In the first case, plants, absorbing CO_2 as a result of their photosynthesis, may reduce the soluble bicarbonate to the insoluble carbonate. In the second, the union of ammonia and CO_2 , resulting from animal metabolism, is thought to produce NH_4CO_3 , the resulting CO_3 ions replacing the Ca of a salt like CaSO_4 again to form CaCO_3 . Recent experimental work by Lipman (66) has shown that ammonia and CO_2 actually do unite under the conditions postulated by Murray and Irvine (77).

While we have seen that there is more calcium carbonate formed by living organisms in warmer seas, it is interesting to note that, according to Wattenberg (121), there is slightly more calcium (as CaO) in Atlantic surface water at higher than at lower latitudes. Here, then, there would be slightly more calcium available for fat formation. Similarly, Cooper (22) has found that there is slightly more calcium in the lower water layers of the English Channel, and my published (125) and unpublished results on the fat-content of North Sea plankton show higher values in the deeper water.

All these observations are in accord with the thesis of a direct correspondence between the formation of fat in organisms and the amount of calcium available in solution. They also imply an inverse relation between fatness and calcification

which has been seen to occur. Actually, some of the most heavily calcified organisms known—reef building corals—have been shown by Yonge (132) to contain fat as a food reserve. The amount, however, is likely to be very small and for *Acropora*, obtained from the Red Sea and kindly sent to me by Dr. Cyril Crossland, I have found this content to be less than 1 per cent of the dry weight of the flesh excluding the skeleton. This low percentage is, thus, in accord with all our other observations from warm seas.

DIFFERENTIATION

Living bodies are separated, often obscurely and rather arbitrarily, chiefly by differences of shape into groups of similar individuals called species. The various species are divided by a physiological difference into two groups, the Animals and the Plants.

In the section on vital velocities I have considered these two groups as living at different rates, the animals beginning with a more complex food and working more towards that part of the metabolic cycle where end-products are produced. Here I would add the important consideration that because animals depend upon plants as a food, they must necessarily have a less total food supply available than have plants.

The different vital rate in animals would lead one to expect greater differentiation in the group, and this is indeed the case, for the majority of animal and plant organisms are distinguished by the development in the former of complex excretory, sensory, locomotor, and alimentary organs absent in the latter.

To continue a consideration of differentiation as applied to animals and plants generally it will be interesting to compare the estimated number of species of plants with those of animals. In 1900, Vines

(119) made an estimate of the plants then known, the figures of which have been rounded off by Scott (103) in the following way:

Angiosperms.....	103,000
Gymnosperms.....	2,500
Vascular cryptogams.....	3,500
Mosses and liverworts.....	7,500
Fungi and bacteria.....	40,000
Lichens.....	5,500
Algae.....	14,000
Total.....	176,000

Now these 176,000 species of plants support all the species of the animal kingdom, of which one sub-class alone—the insects—has been computed at 250,000 by Shipley and McBride (108) at about the same time that the estimate for plants was made. As the metabolic rate of animals is greater than plants, and as their food is less, it is clear that the total bulk of animal tissue must be less than that of plants. Specific differentiation, is therefore, all the more intense in animals. The contrast between animals and plants can then be stated in one way as of greater differentiation at the expense of mass in animals with the attendant circumstances of less food and a greater metabolic rate.

Leaving these general considerations of the two great groups of living organisms, let us turn to the spatial distribution of their marine constituents between the two poles. Gardiner in his book *Coral Reefs and Atolls* (34) says that the total number of plants—algae—on the surface reefs and slopes of any atoll is probably about 150, and he gives the following figures from the "Sealark" Expedition to the Indian Ocean:

	Total	Surf reef	20-35 fms.	36-55 fms.
Rhodophyceae.....	85	53	36	18
Chlorophyceae.....	36	22	21	16
Phaeophyceae.....	13	13	3	2
	134	88	60	36

This luxuriance of form is in sharp contrast to the observation of Rudmose-Brown (98) that "10 or 11 species of algae were taken in 10 fathoms from a single bay in the South Orkneys," or to the result of Holmson's account of the marine and non-marine algae of Spitzbergen (54) where only 62 species were found.

Hensen (46) in his account of the German Plankton Expedition of 1889 gives the numbers and forms of diatoms found at twelve stations on the course of the "National" between July 29th and August 4th. Six of these stations were in the Labrador Current and six a little further to the south in the Florida Stream. In the

Deutschland being relatively close to land during this part of her course.

The Dinophysoidea of the eastern tropical Pacific revealed themselves in collections made by Kofoed and Skogsberg (60) as 132 species out of 198 recognized by the authors as constituting the family. In her *Dinoflagellates of Northern Seas*, Dr. Lebour (64) describes 22 species of this family as inhabiting North Temperate to Boreal-Arctic seas. For a region still further north, Meunier (73) notes only 6 species for the same family.

In the animal kingdom there are some recent surveys of Foraminifera of the Southern Hemisphere by Heron-Allen and

TABLE 3
Relation of number and species of Coccolithophoridae to latitude (Atlantic Ocean)

Approximate latitude	40-45 to 40-25 N.	40-25 to 40-0 N.	30-45 to 30-25 N.	30-05 to 10-45 N.	10-15 to 0-30 N.	0-15N. to 0-30S.	0-45 to 20-20 S.	20-40 to 30-35 S.	30-55 S.
Temperature range (0-100 metres)	11-15	14-18	15.5-21	19-26	15.5-27	19-26	21-26	15-20	5.5-9
Number of species	4	5	8	10	10	11	12	12	7
Number of individuals	638	1191	1418	454	168	990	571	1122	2174

former area there were 40 forms, but in the latter 60.

Perhaps a better example of the relation of number of species of plankton algae to latitude is afforded by Lohmann's (68) centrifuged samples. These were obtained in the Atlantic while on the "Deutschland." In Table 3 I give an extract from his table showing the number and species of Coccolithophoridae occurring per litre of water between the surface and two-hundred metres, together with the approximate latitudes of his stations.

Here the smaller numbers are met with at the most northerly and southerly stations. Though there are more species in the south than actually at the equator it is probable that this is due to the

Earland (50). These surveys show that 419 species were taken at 56 stations in the neighborhood of the Falkland Islands and only 345 at 90 stations near South Georgia. The Falkland Islands lie between 51° and 53°S., in the Sub-antarctic region. They are outside the limit of the pack-ice and the neighboring sea water is of Pacific origin. South Georgia, on the other hand, is surrounded by northward flowing cold antarctic water and is in the pack-ice area, though it lies only a little further south—between 54° and 55°S.

For the Metazoa, Hentschel (48) gives a table of sponge species distribution in the following form:

Arctic	Tropical Atlantic (30 N.-30 S.)	Antarctic
379	428	235

With more regional sub-division, Hert-meyer (42) gives a similar table for the Tunicata:

Arctic	Sub-Arctic	Tropical	Sub-Antarctic	Antarctic
103	433	629	223	42

Concerning the Crustacea, interesting data have been published by Hjort (53) who gives the number of species of Crustacea, chiefly Copepoda, at different depths and temperatures for five stations made in the Atlantic by the "Michael Sars." Two of the stations (50 and 63) were in the Sargasso Sea, one (80) off the Newfoundland Banks, one (90) off the

species, in the second, 84. The records of the *Calanoida* are another interesting commentary on the differentiation into species in warmer habitats. In Sars' work on the Crustacea of Norway (101) he gives the number of species as 67, but more recently Sewell (105), in the results of a very thorough investigation of the same group for the Indian Ocean, has described 377 species.

Fishes are well known to have very many more species in the warmer waters of the world (see for instance Norman, 84). The following list of littoral genera and species of fish from different localities

TABLE 4
Number of species of Crustacea, chiefly Copepoda, at different depths and temperatures
(After Hjort)

DEPTH	STN. 50	STN. 63	STN. 80	STN. 92	STN. 113
0 to 2-300 m.	22 (17.7 to 20.3)	25 (16.7 to 27.3)	16 (7.6 to 11.8)	18 (11 to 16.5)	21 (8.3 to 11.6)
2-300 to 500 m.	22 (13.7 to 17.7)	32 (13.8 to 16.7)	27 (4.6 to 7.6)	12 (10 to 11)	18 (1.1 to 8.3)
500 to 1000 m.	51 (9.7 to 13.7)	27 (6 to 13.8)	34 (3.3 to 4.6)	33 (8.6 to 10.2)	11 (0.5 to 1.1)

south of Ireland and one (113) in the Norwegian Sea north of the Wyville Thomson Ridge. An abstract of these data is reproduced in Table 4, the figures in brackets, following the number of species, being the temperature range in degrees centigrade for the corresponding depth.

There is clearly a general diminution of species as the temperature falls in the parts of the Atlantic covered by these investigations. In the same connection let us compare the species of copepod found by Aurivillius (8) at a number of stations in the sea between Norway and Jan Mayen with those found by Farran (32) at a few stations near one position in the Bay of Biscay. In the first case there were 16

which I have taken from Ekman (29) shows the extent of differentiation in tropical and semi-tropical habitats:

Arctic and Sub-arctic	64 species
North Sea	68 genera
Mediterranean	144 genera
Red Sea	191 genera
West Indies	299 genera
Tropical W. America	256 genera
South Japan	658 species
North Japan (total)	134 species
Australia	344 genera
New Zealand	108 genera

The diminution of species as one goes north in the Northern Hemisphere is well shown in the proportions of the different food fishes caught in the different statistical areas into which the Ministry of

Agriculture and Fisheries divide their annual Sea Fisheries statistics. More species go to make up the returns from southern areas than from those further north.

On land where the habitats are so much less uniform than the sea it is not possible to compare wide areas with respect to the temperature gradient and differentiation. For a stretch of Africa there are, however, censuses of the number of species of forest trees carried out by the Imperial Forestry Institute of Oxford and

the rainfall is heavier, we get 1371 compared with 1240. Here rainfall which appears to be the important factor in the formation of tropical forests does not appear to have had much effect on the differentiation into species.

Hesse (51) has given several groups of land animals in which the greatest differentiation into species appears to have taken place in the tropics. These are shown in Table 5.

MASS AND DIFFERENTIATION

In view of the tendency for specific differentiation to decrease with latitude in the manner already discussed, I think it relevant to commence this section by inviting a consideration of the total fishery yields, shown in Table 6, for the principal countries of the world and divided roughly into areas lying between 30°N.-30°S., north of 30°N., and south of 30°S. These yields, together with those of whale oil, are all expressed in 1,000's of tons and are taken from Schott (102), le Courbe (65) and the *Bulletin Statistique* of the International Council for the Exploration of the Sea (18).

The figures in Table 6 show clearly the inferiority in yield for the tropical area compared with those both north and south of it.

For the Mediterranean I have pointed out (126) that there is an increase in price of fish from west to east which suggests that the fisheries of the western part are more productive than those of the east.

My own work (127) and that of Natterer (80) and Pereira (93) show higher values for estimates of organic matter in the sea water of the western Mediterranean. Thomsen (116) has shown a similar distribution for phosphates. Moreover, the sea temperatures increase eastwards along the Mediterranean. Sparck (112) in his work on the Mediter-

TABLE 5

Groups of land animals in the tropics in which the greatest differentiation into species appears to have occurred

(After Hesse)

<i>Land snails</i>	<i>Tailless batracians</i>
148 Scandinavia	21 Europe
193 Japan	Over 50 British Guiana
463 Jamaica	
614 Cuba	<i>Snakes</i>
80 Tasmania	31 Europe
	38 Trinidad
<i>Butterflies</i>	3 Tasmania
4560 S. America	22 Victoria
716 Europe and Asia N.	42 New South Wales
Himalayas	70 Queensland
400 Europe	
	<i>Birds</i>
<i>Ants</i>	257 Europe
2888 Tropics	580 Borneo
1055 Temperate zones	

published in the 1934 report. I give the figures in order of latitude:

Union of South Africa	455
Southern Rhodesia	883
Northern Rhodesia	972
Uganda	1371

The number of species identified in these areas diminishes with latitude and it seems likely that there is no climatic difference that would be as important as temperature. If we compare Uganda with another tropical district, Nigeria, where

anean produces values for the grammes per square metre of bottom fauna, which, while showing the Mediterranean to be poorer than northern seas, also indicates that it is more fertile at its western end.

	<i>Grams. per m²</i>
East of Italy.....	6
Bay of Algiers.....	18.7
South-east of Portugal.....	266.4
North Europe	300-400
Greenland.....	100

greater as we go north through the areas in the continental slope, but the catch per hundred hours fishing progressively increases and the number of species diminishes.

In Fig. 10 I have illustrated the catch per hundred hours fishing for the Iceland and North Sea grounds by circles whose areas are proportional to this catch. The segments represent the percentage by weight of the components over one per

TABLE 6
World yields in thousands of tons

	FISHERY YIELDS	WHALE OIL	TOTAL
Japan	4635.0	14.6	10042.9
U. S. A. Alaska and Canada.....	1983.0		
N. W. Europe.....	3243.0		
Mediterranean	167.3		
Mexico	6.3	9.8	438.3
Hawaii	4.5		
S. India	141.5		
French Indo-China	160.0		
Straits Settlements	65.1		
Figi	1.4		
Peru	4.0		
Union of South Africa	15.0		
Australia	30.7		
Chile	19.9	4092.7	4132.6
New Zealand	20.0		

In the Mediterranean, therefore, it would appear that we have a case in which conditions are similar to the general latitude gradient.

While the amount of fish landed within different regions generally decreases towards the warmer parts, it is in these latter areas that the greater number of species tend to be landed. The areas set up for the enumerations made in the Sea Fishery returns for England and Wales may be usefully examined in this connection. The figures for 1931, given in Table 7, show that not only is the gross yield

cent, a residual segment containing a figure showing the number of species and categories in the returns that are individually less than one per cent. While the much smaller North Sea catch is doubtless due in part to the longer and more intensive fishing this area has undergone, the greater differentiation of the catch, so well shown in the figure, is a qualitative difference of wider significance. The example is, in short, in conformity with the other cases dealt with in this section and in which mass appears to be inversely related to differentiation.

TABLE 7

Gross yield, catch per hundred hours fishing, and number of species in different areas in the continental slope

REGION		YIELD IN CWTs.	CWTs. PER 100 HOURS FISHING	SPECIES IN RETURNS
Bear Island and Spitzbergen	II B	924,831	2,115	12
Iceland	V A	3,382,343	893	19
Faroe	V B	957,468	457	21
Rockall	VI B	25,025	355	20
W. of Scotland	VI A	880,740	293	28
W. of Ireland	VII B and C	194,574	211	28
S. of Ireland	VII G and K	665,396	188	28
Portugal and Morocco	XIX	1,116	122	14

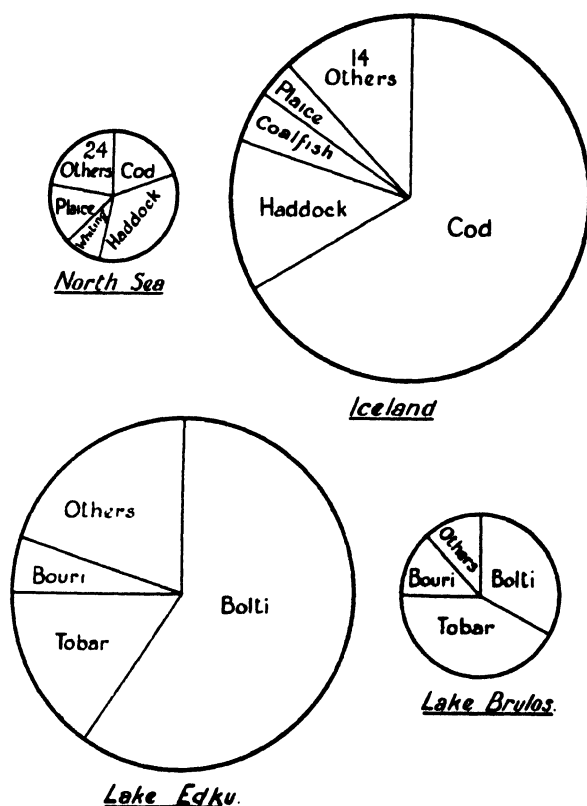


FIG. 10. CATCH PER HUNDRED HOURS FISHING FOR ICELAND AND NORTH SEA GROUNDS AND FOR TWO EGYPTIAN LAKES

Above: circles proportional to the catch per hundred hours 1st class steam trawling in the North Sea and Iceland areas for 1931. *Below:* circles proportional to the mean catch per hectare of two Egyptian lakes for the mean yield of nine post-war years. In all the figures the proportionate weights of the constituent species are shown by the segments.

The relation between mass and differentiation on the one hand and food and temperature on the other, is well shown by the fishery yield of the shallow lakes in the Nile Delta (Fig. 11). Of these lakes, Mariut and Edku in the western delta receive more water and are slightly cooler than those in the east (Wimpenny,

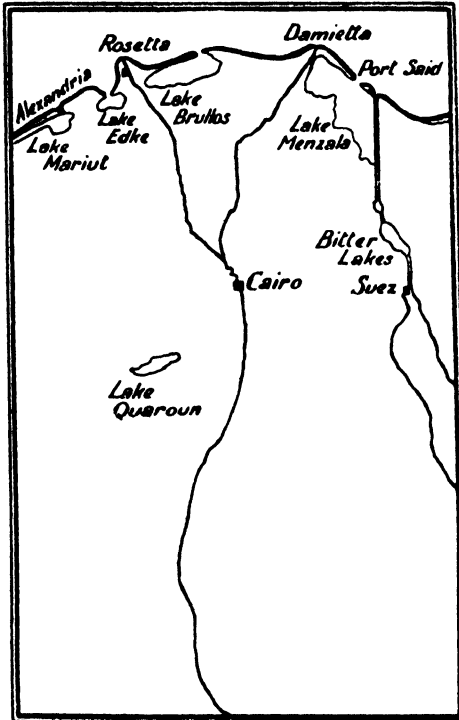


FIG. 11. MAP OF EGYPT SHOWING THE POSITION OF THE DELTA LAKES

128). Their yields and the number of species common enough to enter the market categories are shown in the following list:

Lake	Kgms. for hectare	Species in returns
Mariut	141	9
Edku	279	11
Brullos	60	21
Menzala	64	21

The superior yield and lower differentiation of the cooler lakes with the better food supply is very marked, and in Fig. 10 I have contrasted the extreme cases of Brullos and Edku in the same manner that has been applied to the fisheries of Iceland and the North Sea.

The yield and differentiation into component species for a series of ponds of a Cairo fish farm are shown in Fig. 12 and the areas of the ponds together with the yields per hundred square metres are given in Table 8.

In these ponds the sluices were of the same size and the smaller ponds would therefore have the better food supply per unit area. It is these smaller ponds that furnished the larger yields and whose communities were usually the more simple. The diagram shows that simple communities were also associated with low yield, but in these cases a considerable proportion of the community was made up of predatory species, probably in the process of extinguishing their own food supply.

Further cases bearing on mass and differentiation may be taken from ecological studies on crustacean communities. From work on the copepod fauna of eight rock pools Fraser (33) has given the number of species present and the corresponding densities for each pool. His results are shown in Table 9.

It will be seen that the largest numbers occurred in the pools with only two or three species. The zooplankton of Lake Qarun, which I investigated at fortnightly periods throughout a year (130), was composed of three species of Crustacea. In the cold season, when the catch was far more numerous and the individuals larger, there were virtually only two species present.

Finally, mention must be made of

parasites, which, taking advantage of an easy and abundant food supply, achieve a relatively large size accompanied by loss of differentiation. A curious example of this is *Hemioniscus balanus*. The female of this species (Fig. 13) is found on

number of species and the number of individual in a habitat. The former attributes to Thienemann (115) the fundamental ecological principle that the more extreme, specialized and far from the optimum of the majority of organisms

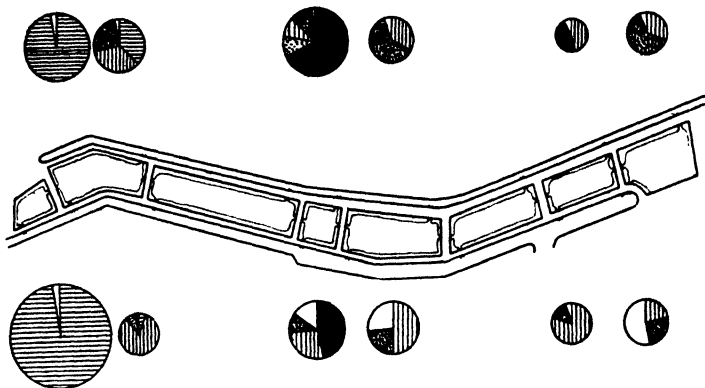


FIG. 12. PLAN OF THE BARRAGE FISH FARM, CAIRO

Above, are circles showing the proportions by weight of the different species per unit area of the corresponding ponds: below, numbers are treated the same way as weights. Horizontal lines indicate "Labees", vertical lines "Bolti", dashes "Bouri", dots "Laffash", and all black "Tobar".

TABLE 8

Areas and yields of a series of ponds of a Cairo fish farm

POND.....	A	B	C	D	E	F	G	H
Area.....	500	1,560	2,090	650	1,575	1,380	956	1,424
Kgms. per 1000 m ²	14.7	9.7	4.7	13.8	6.8	6.1	2.7	5.4

TABLE 9

Copepod fauna of eight rock pools

POOL.....	1	2	3	4	5	6	7	8
Species.....	12	16	6	10	5	2	3	2
Number of copepods per per litre.....	3	30.4	24	41.2	100	12.3	1,769	807

Balanus balanoides and is only recognized as an isopod by the head and first four thoracic segments, the rest of the animal having grown into enormous featureless lobes.

Both Ekman (29) and Hesse (51) refer to the inverse relation between the

is the habitat, the poorer in species but the richer in numbers is the community which inhabits it.

This inverse relation between species and numbers, which appears to be widespread, is particularly well shown in the relations marine organisms of the tropics

bear to those of cooler areas, and in this section I have attempted to show an extension of the relation through numbers to mass. I think we should be cautious, however, before going so far as to define the habitat of the species-poor but numerically rich community of cooler areas "as extreme" and "specialized" in this connection. Particularly in the plankton communities all this extremity and specialization means is lower temperature and richer food supplies. While in the Cairo fish ponds it has been suggested that food supply alone was associated with the simple massive community,

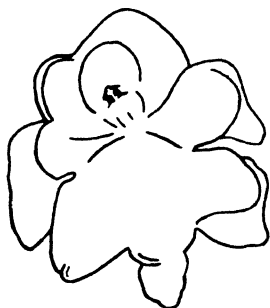


FIG. 13. ADULT FEMALE OF HEMIONISCUS BALANUS

there is little doubt that temperature is an important condition for an internal optimum of assimilation, as it is clear that at its higher levels it must tend to produce an increased vital velocity resulting in differentiation, speciation and a more wasteful use of the available food-supply. Nevertheless the effect of temperature on organisms can seldom be separated from external food supply. In these circumstances I am inclined to replace Thienemann's fundamental principle by a generalization in the following terms: The numbers and mass of organisms tend to vary inversely with the number of species living in any given habitat. Where the habitat conditions remain otherwise the same, a higher temperature

and a lower food supply favors specific differentiation and a reduction of the numbers and total mass of organisms.

INDIVIDUAL SIZE

I want to suggest in this section that, for the bulk but not for all animal forms, there is a tendency for size to increase with latitude. This tendency is also shared by the peridinians. Marine diatoms, however, together with certain animals form a minority group presenting us with the reverse of this phenomenon.

Dealing first with organisms which show an increase of size with latitude, cases of increased individual size within the same species of Foraminifera have been given by Rhumbler (96), while Popoff (95) has shown a decrease in size with rising temperature for the ciliate *Stylonichia mytilus*. For *Cyanea capillata* we have Mayer's (72) measurements showing the superior size of the varieties of this species coming from colder northern waters; and for two other species of medusae, *Aglantha digitalis* and *Phialidium hemisphaericum*, Russell (99) has published measurements showing that the largest individuals originate in the coldest season. Examples from pelagic marine Copepoda given by Steuer (113) may be reinforced by those of Bogorov (15) on the superior length and weight for individuals of *Calanus hyperboreus* and *C. finmarchicus* taken in higher latitudes. In Fig. 14 I have superimposed figures giving the size of some common calanid and euphausiid species upon charts showing the limits of their distribution as established by Mackintosh (71). Here again it is apparent that the sister species in higher latitudes are superior in size. The same conclusion is reached by an inspection of the sizes and limits of distribution for the species of *Sagitta* (Ritter-Zahoney, 97) and

the appendiculate tunicate *Oikopleura* (Lohmann, 69).

Among fish, the herring, anchovy (De Buen, 26), hake (Hickling, 52; Belloc, 12) and Norway haddock can be quoted as species in which the largest individuals come from the highest latitudes. In the case of the herring, there is an exceptionally small race coming from the shallow waters of the White Sea, which may well belong to the minority group for reasons given below. Considering sister

ranges into much higher latitudes than the Sperm Whale, *Physeter macrocephalus*, whose length is given by Silversan (109) as 50-60 feet. There is also the case of the tropical dugongs and manatees, creatures measuring about 8 feet compared with the recently extinct and nearly related *Rhytina stelleri*, which lived in the Arctic and measured 20-30 feet. Among seals, again the largest member of the order, *Macrorhinus leoninus*, comes from the Antarctic polar regions.

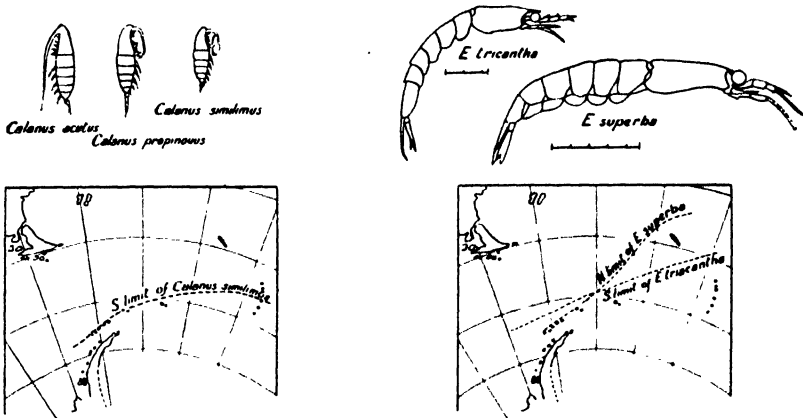


FIG. 14. FIGURES SHOWING CERTAIN SPECIES OF CALANUS AND EUPHAUSIA AND THEIR DISTRIBUTION IN THE ANTARCTIC

species, we have the case of *Cyclone microdon*, which lives in cooler water, and is superior in size to *C. signata* (Hjort, 53). A perusal of Hjort's observations gives a number of other similar cases for oceanic fishes.

Measurements of sea birds given by Alexander (3) show a gradient of size increasing with latitude for the distribution of Penguins, and, using breeding grounds as loci of distribution, for Albatrosses and the seagull genus *Larus*. For marine mammals, I may point out the superior size of *Balaenoptera sibbaldi*, (maximum length, 93 feet, 6 inches, given by Mackintosh and Wheeler, 70) which

In respect of land animals Hesse (51) has called attention to Bergmann's principle, and gives a convincing list of warm-blooded animals, among which, both for related species and for individuals of the same species, a greater size is attained in the colder regions of the area of distribution concerned.

It may now be considered how, in these large and varied sections of the animal kingdom, the circumstance of lower temperature may be connected with an increase of size. Discussing marine animals, Harvey (45) has suggested that the same amount of organic matter could be more economically supported in cold than in

warm habitats. While it has also to be borne in mind that animals generally have more on which to live in colder seas, work has been done which minimizes the importance of food, in so far as its external availability is concerned. Coker (21), working on *Cyclops*, came to the conclusion that low temperature and not food was primarily responsible for increase of size. In this case, the suggestion of an internal optimum for assimilation at a lower temperature is an obvious one to make. Another explanation of the cause of greater size at lower temperatures, has been put forward by Hesse (51) who points out that the onset of maturity is retarded and a longer time is available for somatic growth in these conditions. Lastly, as has been mentioned above, Hesse (51) has adduced examples from among warm-blooded animals, which appear to follow Bergmann's principle (13). This principle contends that larger size is a device to conserve heat, as increase of size in bodies of the same shape decreases the relative radiating surface. It will be understood in this connection, that, while mass increases as the cube of the linear dimension, the surface increases only as the square. Bergmann's principle, it should be noted, does not cover the many instances of cold-blooded animals which have just been dealt with.

A final order of organisms showing this tendency for an increase of size with lower temperature is that of the peridinians. The work of Wesenberg-Lund (112), Bachmann (9), List (67), and Pearsall (92) has shown that the fresh-water *Ceratium hirundinella* decreases in size as the temperature rises. For several species of marine *Ceratium* collected in the South Pacific Ocean, Steeman-Nielson (82) has found the same relation to obtain. The size changes of *Ceratium hirundinella* have been explained by Pearsall (92) as the

result of unusually rapid cell-wall hardening at higher temperatures. According to Pearsall there are two agencies which determine cell size in peridinians, one being wall-hardening and the other cell-turgor, due to the rate of water absorption. Size is the resultant of these two forces, and at higher temperatures, when wall-hardening goes on at a relatively greater rate than cell-turgor, the size of the cell is restricted.

In short, it seems that in peridinians, as in the other forms of this majority group we have now considered, the relative increase of the respiratory function at higher temperatures results in less assimilation and smaller size.

Now let us turn to the minority group in which the larger species and individuals are found in warmer habitats. In the sea, the most striking examples are derived from the tropical coasts. Here are found massive gastropods and the huge lamelli-branch *Tridacna*, replaced towards the poles by smaller molluscs. In a general statement about tubularian hydroids Allmann (1) says "... it may perhaps be asserted that the largest hydroid forms are as a rule confined to the warmer seas, while those of temperate and colder latitudes consist for the most part of humbler and less conspicuous species." According to Parker and Haswell (90) the Actiniaria are also larger in the tropics. An examination of the size of various species of *Balanus* given by Darwin (24) shows that, here too, the largest species, *B. ajax* and *B. psittacus*, both 3.5 inches in diameter are tropical or sub-tropical. While ascidians and echinoderms as a whole appear to belong to the majority group, it may be noticed that Moore (76) has shown an increase in the diameter of the individuals of *Echinus miliaris* for samples taken southwards from Millport through Port Erin to Plymouth.

The position of fishes is somewhat anomalous in respect of the size relation under discussion. Although we have seen individuals of the same species and sister species behaving as if they followed a law which increased their size at lower temperatures, yet, when lists of all the fish over 1,000 pounds in weight, mentioned in Norman and Fraser's book (83), are set down for warm and cold areas, it will be seen that there are six in the former habitat and only one in the latter.

Warm areas	Cold areas
Tunnies	Sturgeons
Spear-fish	
Sail-fish	
Sun-fish	
Sea-devils	
Hammer-heads	

In addition, the largest fish known—*Rhineodon typicus*—is a warm-water form. Discounting the fact that there are more species of fish in the warmer areas, it still appears that these bigger fish favor higher temperatures. We may perhaps search for a clue to their behavior by observing that these giants are all either littoral or pelagic forms and not representative of all the fish communities.

Of terrestrial animals, insects (with the exception of some bumble bees), amphibia, and reptiles all fall into the minority group. In addition, I would add, from among the mammals, bats.

In the case of terrestrial animals, and those which live in shallow coastal water, or near the surface of the sea, I think the diminished size at higher latitudes is most likely to be caused by intermittent growth due to the longer and deeper seasonal fall in temperature. For land animals, the increasing duration and severity of the temperature depression results in progressively longer periods of hibernation for reptiles, amphibians and some mammals (e.g. bats) as the poles are ap-

proached. In insects, the period of pupation is increased. Seasonal diminution of organic production in coastal and superficial areas of the sea may exert a similar effect, reducing the time possible for assimilation to a greater and greater degree as the poles are approached. This effect would be especially marked on organisms with a life of several years, on those unable to pursue their prey (i.e. in particular sedentary forms), or those whose natural food supply is specially affected by seasonal falls of temperature. In the explanation just advanced, there can be little question of size differences being governed by temperature at different latitudes, as the postulated differences in the external food supply robs the conditions for comparison of any uniformity.

To this minority group must also be added certain plants—the pelagic diatoms. Taking the species dealt with in Lebour's *Plankton Diatoms of Northern Seas* (129), it appears that in nineteen genera spread over a wide area and containing species living in warmer and colder habitats, there are thirteen in which the smallest species were found in the colder part of the generic range.

Marine diatoms find their optimum conditions for growth in numbers in the cooler areas, where the sea affords them a better nutrient medium. The explanation of their greater individual size as being due to better external conditions for assimilation seems, therefore, to be excluded. I have made some speculations on this matter in an earlier paper on the size of diatoms (129) which I may here re-state and extend. The cell-walls of cold-water diatoms are thicker than those from the tropics, consequently a few divisions by internal sliding growth would produce a narrower cell than the same number for a thin-walled individual. Moreover, surface tension effects might cause the newly

formed thin-walled auxospore bud to arise at a greater size in warm water. In this connection it should be noted as incidental to the work of Gross (41) that for four species in which auxospore size has been given at different seasons, it was greatest in the warm season for two, showed no difference in one, and was greatest in the cold season for the other. Another possibility is based on the work of Barker (10) which suggests that the effect of rising temperatures may be to increase respiration at a greater rate than photosynthesis. In these circumstances, it seems possible that cells with a relatively high surface-volume ratio (i.e. small cells) might be more rapidly brought to a lethal condition by a rise in temperature than would the larger ones. Larger cells would in fact be favored in warmer seas.

To sum up, although pelagic diatoms resemble some animals in being larger in warmer seas, it is not likely that this resemblance is attributable to the same cause.

SEX

Work on Mendelian inheritance has shown that the production of special chromosomes, or of two kinds of chromosomes and the machinery of reduction division, ensures the production of equal numbers of male and female individuals at fertilization. While this genotypic equality often results in the population of a species of all ages being equally distributed between males and females, it may be subsequently modified by selective mortality or by external causes in such a way as to destroy this balance. A general discussion of cases of this sort has been presented by Goldschmidt (37) and Crew (23), while Geddes and Thompson (35 and 36) have seen in "this" balance of the sexes a metabolic poise in which maleness is nearer the breakdown or katabolic side

and femaleness nearer the anabolic or assimilative side.

If Geddes and Thompson's theory is correct, the effect of increasing temperature might be to increase the ratio of respiration to assimilation towards the upper end of an organism's range of tolerance, and so to produce that relatively katabolic condition they associate with maleness.

However this may be, I have thought it useful to discuss next certain special cases in which I consider temperature likely to bear a significant relation to the sex ratio.

Plants

The alga, *Chara crinita*, and the flowering plant, *Srattotes aloides*, have been shown by Ernst (30) and Wesenberg Lund (123) to produce females only at the northern and colder limits of their distribution.

A coelenterate

The fresh-water medusa, *Craspedacusta sowerbyi* (Fig. 15, reproduced by kind permission of Professor Fernandus Payne), was first recorded by Lankester (62) from a lily pond in Regents Park. The temperature of the pond lay between 25°C. and 30°C. and all the individuals seen were males. Since then it has frequently been recorded in Europe, mainly from aquaria, whither it is suspected of having been introduced with tropical organisms. It has, however, occurred "wild" in a few localities which we may now proceed to examine.

In September, 1929, the species was found in the Exeter Ship Canal (Vallentin, 117) where the temperature was 18°C.-22°C. All the individuals found were males. More recently Tattersall (114) reported the occurrence of the medusae in a reservoir attached to a South Wales colliery. Jenkins (58) in a detailed report of this occurrence showed that the me-

dusae were found from July to September at temperatures between 20°C. and 22°C. Though these temperatures are slightly higher than those at which the medusae were able to make their appearance in the Exeter Ship Canal, it is likely that the

in America, but up to the time of Payne's (88) observations during 1918 in Boss Lake, Indiana, all the occurrences, both in Europe and America, had been males found in aquaria or warm climates. But in Boss Lake all the medusae were females, and the water was "very cold". In a later paper Payne (89) recorded the occurrence of males and females together in the Kentucky River on September 12th, 1925. Since Payne's observations, the medusae have been seen in September, 1933, near Ann Arbor, Michigan, by Woodhead (131). At this most northerly recorded occurrence in the United States "as far as we have been able to determine all individuals were female". In June, 1934, three mature medusae were found at Horseshoe Lake, Quebec Province, in Latitude 46°N. and Longitude 74°25'W. This is the most northerly record yet made for America. Fantham and Porter (31) who reported this occurrence and also another near Rouses Point, New York State, in Latitude 44°58'N. and Longitude 74°25'W. say that all the individuals from both stations were females. The most southerly record from the United States is an old reservoir at Monroe, Louisiana. Here Viosca and Burkinroad (120) record all males, as also does Smith (110) for a habitat in Panama.

Considering the fact that almost always the sex is uniform for each occasion on which the species is found, Payne (89) has suggested that this may be due either to environment or to the fact that each settlement has been due to one introduced hydroid which would be of one sex. On the whole he thought the latter explanation more probable. In the records just presented, however, it has been shown for the United States that females alone have been found in the three northernmost habitats, usually males alone in the central and southern states and that it was

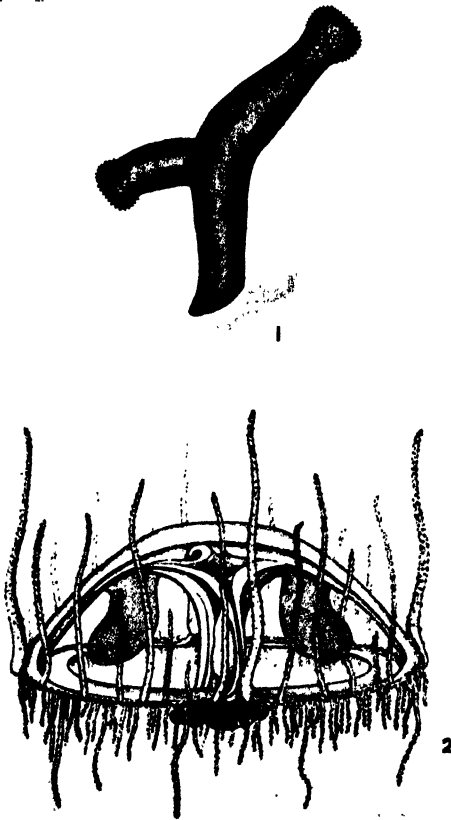


FIG. 15. CRASPEDACUSTA SOWERBYI POLYP ABOVE.
FEMALE MEDUSA BELOW
(From Payne)

South Wales reservoir is a much colder habitat, taking the year as a whole, as its water supply is derived from the neighboring mountains. Bearing this in mind, it is interesting to note that Jenkins finds "All the medusae without exception were females."

C. sowerbyi has been reported frequently

in the central part of the environmental range that both males and females were found together. Moreover, the only record of females from Britain is from a habitat likely to have been exposed to cold influences more than any other. These circumstances do not present a picture such as one would expect to find if the sex of each colony had been determined by the chance introduction of hydroids equally likely to be of one sex or the other. It seems more probable to me that the sex

tions not only of the genus *Limnadia* but also of the genera *Lepidura* and *Apus* made in Africa. *Daphnia pulex* (Olofsson, 85), *Cypridopsis newtoni* (Moniez, 75), *Cypris puberoides* (Vavra, 118), and *Calanus finmarchicus* (Bogorov, 15) have all been shown to have a relative preponderance of females towards the colder limit of their range. Such facts as are known of the distribution by sex for *Rhincalanus gigas* as a result of the work of Ottestad (87), Ruud (100), and Ommanney (86) suggest

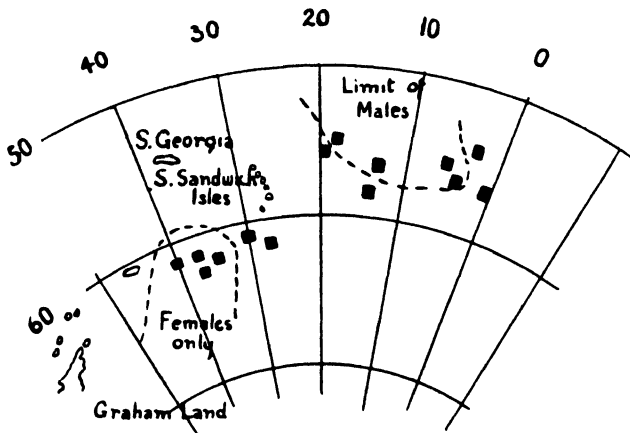


FIG. 16. THE DISTRIBUTION OF RHINCALANUS GRANDIS. "VIKINGEN" STATIONS 1929-30

found is an effect of the environment either upon the hydroid or medusoid persons of the species.

If this is so an investigation into whether the environment could operate directly upon the chromosomal machinery, or whether a selective mortality might be involved, would form suitable aims for a laboratory experiment upon this organism. The most obvious environmental factor is, of course, temperature.

Crustacea

Limnadia lenticularis has not been known to produce males in any number (Brehm, 17), but males are in the majority in collec-

that this species behaves in a similar way (Fig. 16).

Insects

Seiler (104) has shown that the effect of increasing the temperature at which the maturation divisions take place increases the proportion of eggs in which the X chromosome is extruded into the polar body and so increases the proportion of males. Seiler's results may be tabulated in the following way:

Temperature (Centigrade)	X chromo- some in egg	X chromo- some extruded	Sex ratio ♀	♂
3.5	48	31	155	100
18.0	61	45	136	100
35.0-37.0	58	84	62	100

The frog

Goldschmidt (37) quotes experiments of Hertwig and Witschi in which rearing at higher temperatures produced a population predominantly, and in some cases entirely, male. According to Goldschmidt every bisexual individual possesses hormones which can call forth one or the other sex. The sex determining substances act in proportion to their concentration and the times at which they reach their maximum concentrations are obviously very important. In these circumstances it is easy to understand the possible differential effect of some external factor such as temperature acting on the two sex hormones and affecting or reversing the normal ascendancy.

Man

The censuses of human populations show the most abundant array of data on the alteration of the sex ratio with latitude.

Excluding certain countries whence census reports of the sex numbers are difficult to vouch for, as for instance the Anglo-Egyptian Sudan or the Straits Settlements and the Malay States, where there is an unusual distortion of the natural sex ratio due to a large population of immigrants, there is given, in Table 10, a list of 39 populations, set out roughly in order of latitude. It will be seen that in all the populations cited north of Latitude 45°N., whether subject to the mortality of the Great War or not, there were more females than males. Of the ten countries between 45°N. and 35°N., females exceeded males in six countries, and one of them—Spain—is a country which suffered no mortality of males due to the War. Finally, for the thirteen countries included in the zone between 35°N. and 35°S., only three, and these not materially

TABLE 10
Sex ratio and latitude

COUNTRY OR POPULATION	FEMALES PER HUNDRED MALES	CENSUS DATE
Greenland Eskimos.....	109	
Iceland.....	105	1920
Finland.....	103	1920
Norway.....	105	1920
Sweden.....	104	1926
Russia.....	107	1928
Denmark.....	104	1921
Poland.....	107	1921
England.....	109	1931
Germany.....	107	1924
Holland.....	101	1920
France.....	108	1926
Hungary.....	106	1920
Austria.....	108	—
Switzerland.....	107	1930
45°N.		
Serbia.....	104	1921
Portugal.....	111	1920
Spain.....	103	1930
Italy.....	104	1931
Greece.....	103	1921
Roumania.....	98.5	1919
Bulgaria.....	99.5	1927
Turkey.....	107	1927
Japan.....	98	1926
U. S. A. (whites).....	96	1920
35°N.		
Mexico.....	105	1921
Egypt.....	99.5	1917
India.....	95	1911
Ceylon.....	89	1911
Siam.....	100	1919-20
Columbia.....	107	1918
0°		
Brazil.....	98	1920
New Guinea.....	55	1921
Paraguay.....	78	1921
Uruguay.....	82	1926
Chile.....	101	1920
Union of South Africa.....	94	1921
Australia.....	97	1921
35°S.		
New Zealand (excluding Maoris).....	96	1926

is the increasing ratio of males among the white population of South Africa as one goes northward from the point of first settlement at the Cape. These ratios have been shown in Fig. 17 and should be compared with those for the colored races shown in panels on the figure. It is significant to note that the gradient of the sex-ratios is in the same direction for both populations, although it is likely that they have progressively settled into the Union from separate ends. In the United States also it is interesting to note that there are slightly more females per hundred males (98) for the blacks, whose origin is a hotter climate, than for the whites of native parentage (97) who may be considered as having come from a rather cooler area.

Pitt-Rivers (94), as a result of studying vital statistics for Australian aboriginals, Maoris, and Red Indians, has concluded that an increase in masculinity is correlated with a decreasing population. He also considers that the mixing of pure-blood populations results in increase and a drop in masculinity. It is evident that the effect of climate must be distinguished from this conception of Pitt-Rivers, otherwise populations in warm areas would all be dying out and those in the cooler areas increasing. Actually, it appears that one explanation of the increased masculinity of populations in warmer areas is that the length of life is reduced and that, as the mortality rate of males is somewhat greater than females, the shortening of the length of life acts differentially in favor of the male.

Finally, while most of the cases of dying races come from warm climates, there is one case of a community of Norsemen who settled in Greenland and who died out to the accompaniment of increasing cold (55). It is certainly interesting, and perhaps significant, to note that, in these particular

climatic conditions, of 17 bodies whose sex it was possible to determine and which had been taken from graves in this settlement, 10 were women.

CONCLUSION

The evidence of the successive and more complicated living organisms which we know as the evolution theory does not yet include any case of a new species being actually observed to arise. The enormously greater differentiation of the tropical faunas, however, provides circumstantial evidence that the warmer parts of the earth are the most likely cradle for the origin of species.

The study of the chromosomal mechanism and the breeding experiments of geneticists have shown that the segregation of certain genes and the production of a race that will thereafter remain true, may readily occur. In the section on "Sex" we have already seen a case in which temperature has been held to have affected nuclear division with a resultant alteration in the primary sex ratio. In these circumstances we should not find it difficult to expect special segregations of genes or "mutants" to take place more often in lower latitudes. It should be noted that such a view of the origin of species implies a segregation and differentiation of characters already present in the original stock and is therefore analytic rather than synthetic.

However the differentiation into the large number of species now living may have been brought about, in view of our observations on the distribution of animals on the globe, it seems likely that temperature must have played a great part. During that part of the earth's history during which living organisms have been present, there have been warm and cold periods (glacial and inter-glacial epochs) and it may well be that the great-

est numbers of new species were formed in the warm interglacial epochs.

A more immediate application of the deductions made in this paper applies to the problem of over-fishing. In the North Sea, a smaller yield of food-fish is being made for unit time and gear than was formerly the case, and most fishery scientists are agreed that over-fishing is the cause of this condition. Apart from the gross decline of the yield there has also been a change in the relative importance of the species. While, for instance, cod, haddock, and halibut, all northern fish, have declined steadily (18) in the post-war years, two southern ones have increased in importance. The whole catch

has declined because the northern species are still the greatest part of the yield. Now this qualitative change might have been of no significance had it not been recently pointed out by Scherhag (106) that a continuous warming up, is going on in the Northern Hemisphere. In these circumstances it appears impossible to say that the reduced yield per unit of effort in the North Sea is due solely to over-fishing. The possibility that the rising temperature is causing an increase in the specific complexity and a decrease in individual size and total bulk in the way that has been suggested in the previous pages remains to be examined as at least a contributory cause.

LIST OF LITERATURE

- (1) ALLMAN, G. J. A Monograph of the Gymnoblasic or Tubularian Hydroids. Part II. *Ray Society Monographs*, pp. 235-450, 1871.
- (2) AHMAD, B. Observations on a diatom (*Nitzschia closterium* W.Sm.) as a source of vitamin A. *Biochem. Jour.*, 24, pp. 860-865, 1930.
- (3) ALEXANDER, W. B. Birds of the Ocean. *New York and London*, (Putnam's Sons), 428 pp., 1928.
- (4) TENTH ANNUAL REPORT of the Imperial Forestry Institute. *Oxford*, 36 pp., 1934.
- (5) APPELLÖF, A. Invertebrate Bottom Fauna. Chapter VIII, pp. 457-560, in Murray and Hjort, *Depths of the Ocean*. *London* (Macmillan Co.), 1912.
- (6) ATKINS, W. R. G. The phosphate content of sea water in relation to the growth of the algal plankton. Part III. *Jour. Mar. Biol. Assoc.*, 14, p. 447-457, 1926.
- (7) —. Seasonal variations in the phosphate and silicate content of sea-water in relation to the phytoplankton crop. Part V. November, 1927, to April, 1929, compared with earlier years from 1923. *Jour. Mar. Biol. Assoc.*, 16, pp. 821-852, 1930.
- (8) AURIVILLIUS, C. W. S. Animalisches Plankton aus dem Meere zwischen Jan Mayen, Spitzbergen, K. Karls Land und der nordkuste Norwegens. *Kongl. Sveriska Vetenskaps-Akad. Handlingar*, Bd. 32, No. 6, 71 pp., 1899.
- (9) BACHMANN, H. Das Phytoplankton des Süßwassers mit besonderer Berücksichtigung des Vierwaldstättersees. *Jena* (Gustav Fischer), 213 pp., 1911.
- (10) BARKER, H. A. Photosynthesis in diatoms. *Arch. f. Mikrobiol.*, 6, pp. 141-156, 1935.
- (11) BECKING, L. B., TOLMAN, C. F., McMILLAN, H. C., and HASHIMOTO, T. Preliminary statement regarding the diatom "epidemics" at Copalis Beach, Washington, and an analysis of diatom oil. *Econ. Geology*, 22, pp. 356-368, 1927.
- (12) BELLOC, G. Étude monographique du merlu *Merluccius merluccius* L. *Rev. des Travaux de l'Office des Pêches Mar.*, *Rev. Trimestr.*, 2, pp. 153-199: 231-288, 1921.
- (13) BERGMANN, C. Ueber die Verhältnisse der Wermeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, pp. 595-708, 1847.
- (14) BIRGE, E. A., and JUDAY, C. The Inland Lakes of Wisconsin. The Plankton. I. Its Quantity and Composition. *Wisconsin Geolog. and Nat. Hist. Survey, Bulletin* 64, pp. 222, 1922.
- (15) BOGOROV, B. G. Seasonal changes in biomass of *Calanus finmarchicus* in the Plymouth area in 1930. *Jour. Mar. Biol. Assoc.*, 19, pp. 585-612, 1934.
- (16) BRANDT, K. Beiträge zur Kenntniss der chemischen Zusammensetzung des Planktons. *Wiss. Meeresuntersuch.*, *Kiel*, 3, pp. 43-90, 1898.
- (17) BREHM, V. Das Plankton der Tropenseen. *Int. Rev. Hydrobiol.*, 10, pp. 160-165, 1922.

- (18) CONSEIL INTERNATIONAL pour l'Exploration Scientifique de la Mer. *Bulletin Statistique*, 11-24, 1919-1934.
- (19) CHILD, C. M. Individuality in Organisms. *Chicago* (University of Chicago Press), 213 pp., 1915.
- (20) CLOWES, G. H. A. Protoplasmic equilibrium. *Jour. Phys. Chem.*, 20, pp. 407-451, 1916.
- (21) COCKER, R. E. Influence of temperature on size of fresh-water copepods (*Cyclops*). *Int. Rev. Hydrobiol.*, 29, pp. 406-436, 1933.
- (22) COOPER, L. H. N. The variation of excess base with depth in the English Channel with reference to the seasonal consumption of calcium by plankton. *Jour. Mar. Biol. Assoc.*, 19, pp. 747-754, 1934.
- (23) CREW, F. A. E. Animal Genetics; an Introduction to the Science of Animal Breeding. *London and Edinburgh* (Oliver and Boyd), 420 pp., 1925.
- (24) DARWIN, C. A Monograph on the Sub-class Cirripedia—Balanidae. *Ray Society Monographs*, pp. 1-495, 1854.
- (25) DRACON, G. E. R. A General Account of the Hydrology of the South Atlantic Ocean. *Discovery Reports*, 7, pp. 171-238, 1933.
- (26) DE BURN, F. Rapport sur les Clupéides et leur Pêche (4^e. Rapport). *Rapp. et Proc.-Verb. des Réunions Comm. Int. pour l'Explor. Scient. de la Mer Méditerranée*, 6, pp. 289-336, 1931.
- (27) DELFF, C. Beiträge zur Kenntnis der chemischen Zusammensetzung wirbelloser Meerestiere. *Wiss. Meeresuntersuch.*, *Kiel*, 14, pp. 51-81, 1912.
- (28) EARLAND, A. Foraminifera. Part II. South Georgia. *Discovery Reports*, 7, pp. 27-138, 1933.
- (29) EKMAN, S. Tiergeographie des Meeres. *Leipzig* (Akademische Verlagsgesellschaft M. B. H.), 542 pp., 1935.
- (30) ERNST, A. Experimentelle Erzeugung erblicher Parthenogenesis. *Zeit. Indukt. Abstammungs- u. Vererbungslehre*, 17, pp. 203-250, 1917.
- (31) FANTHAM, H. B., and PORTER A. Occurrence of the fresh-water medusa, *Craspedacusta sowerbii*, in eastern Canada. *Nature*, 14, pp. 515-516, 1938.
- (32) FARRAN, G. P. Biscayan plankton collected during a cruise of H.M.S. 'Research', 1900. Part XIV. The Copepoda. *Jour. Linn. Soc., Zoology*, 36, pp. 219-310, 1926.
- (33) FRASER, J. H. The distribution of rock pool Copepoda according to tidal level. *Jour. Animal Ecology*, 5, pp. 23-28, 1936.
- (34) GARDINER, J. STANLEY Coral Reefs and Atolls. *London* (Macmillan Co.), 181 pp., 1931.
- (35) GEDDES, P., and THOMSON, J. A. The Evolution of Sex. *London* (Walter Scott), 322 pp., 1889.
- (36) —, and —. Sex. *London* (Williams and Norgate), 255 pp., 1927.
- (37) GOLDSCHMIDT, R. (translated by W. J. Dakin). The Mechanism and Physiology of Sex Determination. *London* (Methuen and Co.), 259 pp., 1923.
- (38) GRAN, H. H. The plankton production of the North European waters in the spring of 1912. *Bull. Planktonique pour l'année 1912, Cons. Int. pour l'Explor. de la Mer*, pp. 1-142, 1915.
- (39) —. Studies on the biology and chemistry of the Gulf of Maine. II. Distribution of phytoplankton in August, 1932. *Biol. Bull.*, 64, pp. 159-182, 1933.
- (40) GRAHAM, M. Phytoplankton and the herring. Part III. Distribution of phosphate in 1934-1936. *Min. Agric. Fish., Fish. Invest.*, Ser. II., 16, No. 3, 26 pp., 1938.
- (41) GROOM, F. The life history of some marine plankton diatoms. *Phil. Trans. Roy. Soc. London*, Ser. B., 228, pp. 1-47, 1937.
- (42) HARTMEYER, R. Tunicata. Bronn's Klassen und Ordnungen des Tier-reichs, III Supplement, Abt. 1, pp. 1281-1773, 1911.
- (43) HARVEY, H. W. Oxidation in sea water. *Jour. Mar. Biol. Assoc.*, 13, pp. 953-969, 1925.
- (44) —. Nitrate in the sea. *Jour. Mar. Biol. Assoc.*, 14, pp. 71-88, 1926.
- (45) —. Biological Chemistry and Physics of Sea Water. (Cambridge University Press), 194 pp., 1928.
- (46) HENSEN, V. Einige Ergebnisse der Expedition. *Ergb. Plankton-Exp. d. Humboldt-Stiftung*, Bd. I., pp. 18-46, 1892.
- (47) HENTSCHEL, E. Allgemeine Biologie des Südatlantischen Ozeans. *Wiss. Ergeb. Deutsch. Atlant. Exped. Forsch.-u. Vermess.-Schiff "Meteor"*, 11, pp. 1-344, 1936.
- (48) —. Die Kiesel- und Hornschwämme des nördlichen Eismere. *Fauna Arctica*, 5, pp. 857-1042, 1919.
- (49) HERODOTUS. The History. Book III, Rawlinson's translation. *London* (Everyman's Library), 2 vols., pp. 382; 366, 1910.
- (50) HERON-ALLEN, E., and EARLAND, A. Foraminifera. Part I. The Icefree Area of the Falkland Islands and Adjacent Seas. *Discovery Reports*, 4, pp. 291-460, 1932.
- (51) HESS, R. Ecological Animal Geography. (Translated and prepared by W. C. Allee and K. P. Schmidt), *New York* (John Wiley and

- Sons); *London* (Chapman and Hall), 597 pp., 1937.
- (52) HICKLING, C. F. The natural history of the hake. Part III. Seasonal changes in the condition of the hake. *Min. Agric. and Fish., Fish. Invest.*, Ser. II., 12, No. 1, 78 pp., 1930.
- (53) HJORT, J. Pelagic Animal Life. Chapter IX, pp. 561-659, in Murray and Hjort, *Depths of the Ocean*. *London* (Macmillan Co.), 1912.
- (54) HOLMBOM, H. R. Exploration du Nord-Ouest du Spitzberg entreprise sous les auspices de S.A.S. le Prince de Monaco par la Mission Isachsen. Cinquième Partie. Observations Botaniques. *Rés. Camp. Scient. Albert ler de Monaco*, Fasc. 44, 81 pp., 1913.
- (55) HØVGAARD, W. The Norsemen in Greenland. Recent discoveries at Herjolfsnes. *The Geographical Review*, 15, pp. 605-616, 1925.
- (56) IVANOFF, L. A. Sovremenoe sostoyaniye voprosa ozasukhustoičivost'i rastenii. (The present state of the question of drought resistance.) *Bull. App. Botany and Plant Breeding, Leningrad*, B. 13, pp. 3-32, 1923.
- (57) JOHNSTONE, J. Conditions of Life in the Sea. (Cambridge University Press), 332 pp., 1908.
- (58) JENKINS, H. The occurrence of the fresh-water medusa, *Craspedacusta sowerbii*, Lankester, in Monmouthshire. *Trans. Cardiff Nat. Soc.*, 68, pp. 39-45, 1935.
- (59) KNIP, H. Ueber die Assimilation und Atmung der Meeresalgen. *Int. Rev. d. ges. Hydrobiol.*, 7, pp. 1-38, 1914.
- (60) KOPOID, C. A., AND SKOOSBERG, T. The Dinoflagellata: The Dinophysoidae. *Mem. Mus. Comp. Zool., Harvard*, 51, 766 pp., 1928.
- (61) KREBS, E., AND VERJINSKAYA, N. Seasonal changes in the phosphate and nitrate content and in hydrogen ion concentration in the Barents Sea. *Jour. du Cons.*, 5, pp. 329-346, 1930.
- (62) LANKESTER, E. R. On *Limnocoedium* (*Craspedacusta*) *sowerbii*. A new Trachomedusa inhabiting fresh water. *Quart. Jour. Micr. Sci.*, 20, pp. 351-371, 1880.
- (63) LEATHES, J. B., AND RAPER, H. S. The Fats. Monographs on Biochemistry, 2nd Edition, *London* (Longmans, Green and Co.), 242 pp., 1925.
- (64) LEBOUR, M. V. The Dinoflagellates of Northern Seas. *Plymouth* (Marine Biological Association), 250 pp., 1915.
- (65) LECOURBE, G. Rapport sur la statistique. *Rapp. Proc.-Verb., Comm. Int. Explor. de la Mer Médit.*, 3, pp. 157-159, 1928.
- (66) LIPMAN, C. B. A critical and experimental study of Drew's bacterial hypothesis on CaCO_3 precipitation in the sea. *Papers from the Dept. of Mar. Biol., Carnegie Institute of Washington*, 19, pp. 179-191, 1924.
- (67) LIST, T. Ueber die Temporal- und Lokalvariation von *Ceratium hirundinella* O. F. M. aus dem Plankton einiger Teiche in der Umgegend von Darmstadt und einiger Kolke des Altrheins bei Erfelden. *Arch. f. Hydrobiol. u. Planktonk.*, 9, pp. 81-126, 1914.
- (68) LOHMANN, H. Untersuchungen über das Pflanzen- und Tierleben der Hochsee, zugleich ein Bericht über die biologischen Arbeiten auf der Fahrt der "Deutschland" von Bremerhaven nach Buenos Aires. *Veröffentl. d. Inst. f. Meereskunde*, N. F., A. *Geogr.-naturwiss. Reihe* Heft 1, 92 pp., 1912.
- (69) —. Appendicularien. *Nordisches Plankton, Zool. Teil*, 2, pp. 11-21, 1901; 23-29, 1911.
- (70) MACKINTOSH, N. A., AND WHEELER, J. F. G. Southern Blue and Fin Whales. *Discovery Reports*, I, pp. 257-540, 1929.
- (71) —. Distribution of the Macroplankton in the Atlantic Sector of the Antarctic. *Discovery Reports*, 9, pp. 65-160, 1934.
- (72) MAYER, A. G. Medusae of the World. Volume III. The Scyphomedusae. *Publ. 109, Carnegie Institute of Washington*, pp. 495-735, 1910.
- (73) MEUNIER, A. Microplankton des Mers de Barents et de Kara. Duc d'Orleans, Campagne Arctique de 1907, 355 pp., 1910.
- (74) MINISTRY OF AGRICULTURE AND FISHERIES. Sea Fisheries Statistical Tables, 1931, 49 pp., (1932).
- (75) MONIEZ, R. L. Les mâles chez les Ostracodes d'eau douce. *Rev. Biol. Nord. France*, 3, No. 9, pp. 354-356, 1891.
- (76) MOORE, H. B. A comparison of the biology of *Echinus esculentus* in different habitats. Part III. *Jour. Mar. Biol. Assoc.*, 21, pp. 711-719, 1937.
- (77) MURRAY, J., AND IRVINE, R. On coral reefs and other carbonate of lime formations in modern seas. *Proc. Roy. Soc. Edin.*, 17, pp. 79-109, 1889-90.
- (78) MURRAY, Sir J. The distribution of organisms in the hydrosphere as affected by varying chemical and physical conditions. *Int. Rev. Hydrobiol.*, 1, pp. 10-17, 1908.
- (79) —. Depths and Deposits of the Ocean. Chapter IV in Murray and Hjort, *Depths of the Ocean*, pp. 129-209, *London* (Macmillan Co.), 1912.

- (80) NATTERER, K. Chemische Untersuchungen im östlichen Mittelungen. I-IV. Reise S. M. Schiffes Pola in den Jahren 1890-93. *Wien A. K. Denkschr.* 60. *Ber. d. Comm. f. Erforsch. d. Ost. Mittelmeers*, 1893.
- (81) NICHOLLS, A. G. On the biology of *Calanus finmarchicus*. I. Reproduction and seasonal distribution in the Clyde sea-area during 1932. *Jour. Mar. Biol. Assoc.*, 19, pp. 83-109, 1933.
- (82) NIELSEN, E. STERMANN. Untersuchungen über die Verbreitung, Biologie und Variation der Ceratium im südlichen Stillen Ozean. *Dona-Report*, No. 4, 67 pp., 1934.
- (83) NORMAN, J. R., AND FRAYER, F. C. Giant Fishes, Whales and Dolphins. *London* (Putnam's Sons), 361 pp., 1937.
- (84) —. A History of Fishes. *London* (Ernest Benn Ltd.), 463 pp., 1931.
- (85) OLOFSSON, O. Studien über die Süßwasserfauna Spitzbergens. Beitrag zur Systematik, Biologie und Tiergeographie der Crustaceen und Rotatorien. *Zool. Bidrag*, 6, pp. 183-646, 1918.
- (86) OMMANNEY, F. D. *Rhinocalanus gigas* (Brady), a copepod of the southern macroplankton. *Discovery Reports*, 13, pp. 277-384, 1936.
- (87) OTTESTAD, P. On the biology of some southern Copepoda. *Hvalradets Skr.*, No. 5, 61 pp., 1932.
- (88) PAYNE, F. A study of the fresh-water medusa, *Craspedacusta ryderi*. *Jour. Morph.*, 38, pp. 387-430, 1924.
- (89) —. Further studies on the life history of *Craspedacusta ryderi*, a fresh-water hydro-medusan. *Biol. Bull.*, 50, pp. 433-443, 1926.
- (90) PARKER, T. J., AND HASWELL, W. A. A Text-book of Zoology, Third Edition, Vol. I, 816 pp., *London* (Macmillan Co.), 1921.
- (91) PRERRELL, W. H. Phytoplankton and environment in the English lake district. *Rev. Algolog.*, I, pp. 53-67, 1924.
- (92) —. Form variation in *Ceratium hirudinella* O. F. M. *Proc. Leeds Phil. Soc.*, I, pp. 432-439, 1929.
- (93) PEREIRA, J. G. Determinación de materia orgánica en las aguas de mar. *Notas y Resúmenes*, Ser. 11, No. 4, 25 pp., 1924.
- (94) PITT-RIVERS, G. H. L. -F. The Clash of Culture and the Contact of Races: An Anthropological and Psychological Study of the Laws of Racial Adaptability, with Special Reference to the Depopulation of the Pacific and the Government of Subject Races. *London* (George Routledge and Sons, Ltd.), 312 pp., 1927.
- (95) POPOFF, M. Experimentelle Zellstudien. *Arch. Zellforsch.*, I, pp. 245-379, 1908.
- (96) RHUMBLER, L. Die Foraminiferen (Thalamophoren) der Plankton-Expedition. Zugleich Entwurf eines natürlichen Systems der Foraminiferen auf Grund selektionistischer und mechanisch-physiologischer Faktoren. Erster Teil: Die allgemeinen Organisationsverhältnisse der Foraminiferen. Zweiter Teil: Systematik: *Arrhabdammidia*, *Arammodiscidlia* und *Arnodosammidia*. *Ergeb. Plankton-Exped., Humboldt-Stiftung*, III. L. c. pp. 1-331, 1911; pp. 332-476, 1913.
- (97) RITTER-ZAHONY, R. VON. Chaetognathi. Das Tierreich, Lfg. 29, 35 pp., 1911.
- (98) RUDMOSE-BROWN, R. N. The Polar Regions. *London* (Methuen), pp. 255, 1927.
- (99) RUMBLE, F. S. A review of some aspects of zooplankton research. *Rapp. Proc.-Verb., Cons. Int.*, 45, pp. 3-30, 1936.
- (100) RUUD, J. Nitrates and phosphates in the Southern Seas. *Jour. du Cons.*, 5, pp. 347-360, 1930.
- (101) SARR, G. O. The Crustacea of Norway. Vol. 4. Copepoda: Calanoida. 171 pp., 1903.
- (102) SCHOTT, G. Geographie des Indischen und Stillen Ozeans. *Hamburg* (C. Boysen), 413 pp., 1935.
- (103) SCOTT, D. H. The Evolution of Plants. *London* (Williams and Norgate), 256 pp., 1911.
- (104) SMILER, J. Geschlechtschromosomenuntersuchungen an Psychiden. I. Experimentelle Beeinflussung der geschlechtsbestimmenden Reifeteilung bei *Talaeporia tubulosa* Retz. *Arch. f. Zellforsch.*, 15, pp. 249-268, 1920.
- (105) SEWELL, R. B. S. The Copepoda of Indian Seas. Calanoida. *Mem. Indian Museum*, 10, pp. 1-221, 1929; pp. 223-407, 1932.
- (106) SCHERHAG, R. Die Erwärmung der Arktis. *Jour. du Cons.*, 12, pp. 263-276, 1937.
- (107) SHERMAN, H. C., AND QUINN, E. J. The phosphorus content of the body in relation to age, growth and food. *Jour. Biol. Chem.*, 67, pp. 667-677, 1926.
- (108) SHIPLEY, A. E., AND MACBRIDE, E. W. Zoology. (Cambridge University Press), 632 pp., 1901.
- (109) SALVESEN, T. E. The whale fisheries of the Falkland Islands and dependencies. *Sci. Res., Scot. Nat. Antarctic Exped.*, 4, pp. 475-486, 1914.
- (110) SMITH, F. Fresh-water Medusae in the Panama Canal Zone. *Science*, 61, pp. 588-9, 1925.
- (111) SMITH, G. The life-cycle of *Cladocera*, with remarks on the physiology of growth and

- reproduction in Crustacea. *Proc. Roy. Soc.*, B. 88, p. 418-435, 1915.
- (112) SPÄRCK, R. Some Quantitative Investigations on the Bottom Fauna at the West Coast of Italy, in the Bay of Algiers, and at the Coast of Portugal. *Rep. Danish Oceanogr. Exped., 1908-1910, to the Mediterranean and Adjacent Seas*. No. 10, Vol. 3 (*Miscellaneous Papers*), 7, 11 pp., 1931.
- (113) STEUER, A. Planktonkunde. *Leipzig and Berlin* (B. G. Teubner), 723 pp., 1910.
- (114) TATTERSALL, W. M. Occurrence of *Craspedacusta sowerbii* Lankester, in Monmouthshire. *Nature*, 132, p. 570, 1933.
- (115) THIENEMANN, A. Lebensgemeinschaft und Lebensraum. *Naturwiss. Wochenschrift.*, N. F. 17, pp. 281-290; 295-303, 1918.
- (116) THOMSEN, H. Nitrate and Phosphate Contents of Mediterranean Water. *Rep. Danish Oceanogr. Exped., 1908-1910, to the Mediterranean and Adjacent Seas*. No. 10, Vol. III (*Miscellaneous Papers*), 6, 14 pp., 1931.
- (117) VALLENTIN, R. Occurrence of *Craspedacusta* (Limnocoedium) *sowerbii* in the Exeter Ship Canal. *Nature*, 125, pp. 15-16, 1930.
- (118) VAVRA, V. Die Süßwasser-Ostracoden Deutsch-Ost-Afrikas. *Thierwelt Ost.-Afrik.*, 4, 28 pp., 1897.
- (119) VINES, S. H. Address to the Botanical Section of the British Association. *Bradford*. 1900.
- (120) VIOUCA, P., AND BURKENROAD, M. D. The fresh-water medusa in Louisiana. *Science*, 84, pp. 155-156, 1936.
- (121) WATTENBERG, H. Ueber den Kalkgehalt des Ozeanwassers. II Mitteilung: Die Verteilung im Atlantischen Ozean. *Ann. d. Hydrog. u. Maris. Meteor.*, 59, pp. 273-277, 1931.
- (122) WESSENBERG-LUND, C. J. Plankton Investigations of the Danish Lakes. Vol. II. General Part. The Baltic Freshwater Plankton, its Origin and Variation. *Copenhagen*, 389 pp., 1908.
- (123) —. Ueber einige eigentümliche Temperaturverhältnisse in der Litoralregion der baltischen Seen und deren Bedeutung, nebst einem Anhang über die geographische Verbreitung der zwei Geschlechter von *Stratiotes aloides*. *Int. Rev. d. ges. Hydrobiol.*, v, pp. 287-316, 1912.
- (124) WEST, G. S. *Algae*. Vol. I., Myxophyceae, Peridiniaceae, Bacillariaceae, Chlorophyceae, together with a brief summary of the Occurrence and Distribution of Freshwater Algae. (Cambridge University Press), 475 pp., 1916.
- (125) WIMPENNY, R. S. Preliminary Observations on the Fat-Content of the Plankton on the English Herring Grounds in the North Sea. *Min. Agric. and Fish., Fish. Invest.*, Ser. 2, 11, No. 5, 23 pp., 1929.
- (126) —. Report on the Fisheries of Egypt for the Year 1928. *Cairo*, Government Press, 86 pp., 1930.
- (127) —. Some Hydrographic Data from the Suez Canal, 1928-29. *Coastguards and Fisheries Service, Egypt, Fisheries Research Section, Bull.* 1, 7 pp., 1930.
- (128) —. The fisheries of Egypt. *Sci. Progress*, 29, pp. 210-227, 1934.
- (129) —. The size of diatoms. I. The diameter variation of *Rhizosolenia styliformis* Brightw. and *R. alata* Brightw. in particular and of pelagic marine diatoms in general. *Jour. Mar. Biol. Assoc.*, 21, pp. 29-60, 1936.
- (130) —, AND TITTERINGTON, E. The Tow-net Plankton of Lake Qarun, Egypt, December 1930 to December 1931. *Ministry of Commerce and Industry, Egypt. Fish. Res. Directorate. Notes and Memoirs* No. 14, 57 pp., 1936.
- (131) WOODHEAD, A. E. Occurrence of fresh-water medusae in Michigan. *Science*, 78, p. 479, 1933.
- (132) YONGE, C. M. Studies on the Physiology of Corals. III. Assimilation and Excretion. *Sci. Reports, Great Barrier Reef Expedition*, 1928-29, I, pp. 83-91, 1931.





COMPARATIVE HEMATOLOGY AND THE FUNCTIONS OF THE LEUCOCYTES

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INTRODUCTION

DESPITE the large bibliography on the blood of the vertebrates the problem of the functions of the leucocytes has not been solved. A final solution of this problem will likely be found only through a thoroughgoing study of the peculiarities of the blood of lower forms, through building up a whole picture of blood, not merely of that portion of it represented by the vertebrates. There is an amazing variation in the wandering cells and blood cells of the series of animals from sponges to man, and yet certain similar types of cells are found throughout the series. Although there is need for much more work on the blood of the invertebrates, a comparative analysis of the information available, if not conclusive, is at least suggestive as to the primitive functions of blood in animals generally.

Sponges

The sponges have no true blood or blood vessels but the parenchyma or mesenchyme occupying the space between the epidermis and the canal system has a variety of cells some of which are free wandering cells. These have separated from an earlier syncytium (Wilson '35). According to Wilson and Penny ('30) some of them are nucleolate, sluggishly amoeboid cells, which vary in appearance. At one end of the nucleolate series the cells are

small (about $5\ \mu$) and free from inclusions; at the other end of the series the cells are larger ($10\ \mu$) and have inclusions. The small nucleolate cells without inclusions are similar in appearance to vertebrate large lymphocytes and hemocytoblasts. They are primitive cells that differentiate into other cell types. To these smaller hyaline cells without inclusions but with distinctly nucleolate nuclei link on serially other types of mesenchyme cells. The primitive nucleolate cells may in fact differentiate into any type of cell in the sponge.

Some of the nucleolate cells with inclusions are doubtless to be looked upon as macrophages since Wilson and Penny state that the inclusions in some of the larger ones indicate that they may be phagocytes. Furthermore, Penny ('33) finds that nucleolate cells ingest degenerating cells and Wilson ('35) says that the digestion of degenerating nuclei in the metamorphosing sponge seems to be under the influence of the nucleolate cells. I have observed neutral red staining vacuoles in them.

Other wandering cells in the sponge parenchyma, of some species at least, include "gray cells" and "globoferous cells." The gray cells have a non-nucleolate nucleus and in the cytoplasm are small granules which are gray in the living cells and which stain with methylene blue and with Nile blue sulphate. They appear to be reserve food since they are used up

in regeneration of sponges from dissociated cells. I have observed that the granules are negative to neutral red. The globiferous cells are also non-nucleolate cells. The cytoplasm contains one larger homogeneous inclusion and several smaller ones. I have observed other cells, not reported by Wilson and Penny, in teased living tissue of *Microciona prolifera*. They have small vacuoles containing brownian granules that stain with neutral red.

(Koehring '30) has produced evidence to show that the neutral red reaction in vacuoles indicates proteolytic enzyme activity. Throughout this paper her thesis is tentatively accepted.)

Sponges have no enteric canal into which food is passed for digestion and for diffusion. There seems to be general agreement among students of sponges that the wandering cells of the sponge parenchyma are the principal participants in the nutrition of the organism. In some sponges the amoebocytes share with the porocytes and the choanocytes the function of capturing and digesting food while in others the function of ingestion and digestion, which is largely intracellular, may be taken over almost entirely by the amoebocytes of the parenchyma. For further details concerning digestion in sponges see Lendenfeld (1890), Minchin (1900), Cotte (1904), Van Trigt (1919).

Coelenterates

The coelenterates have no blood vessels and they do not have so extensive mesenchyme or parenchyma as the sponges, but in many forms the middle layer or mesoglea contains wandering cells. I know of no information relative to the existence among these of primitive cells of totipotent capacities although the ectoderm in some cases, the endoderm in others, proliferates nucleolate cells capable of giving rise to asexual or sexual individuals

(Braem '08, Hargitt '16). Some of the wandering cells of the mesoglea are phagocytic and nutritive in function. Digestion is begun in the coelenteron through the action of an extracellular protease, which breaks down proteins to polypeptids but not to amino acids, and is completed in the endoderm and wandering cells by intracellular enzymes (Metschnikoff, 1880, Boschma, '25, Yonge, '31, Smith, '37, *et al.*). Smith states that "Nutriment is carried to different parts of the body, and excretory products to the gastric filaments and pleated membranes by wandering cells which pass through the mesoglea." In his animals fed with fish blood corpuscles, partially digested corpuscles were to be seen in the cells of the gastric filaments and in wandering cells at the bases of the filaments and in the mesoglea. Runnström ('29) also notes the presence of wandering cells that carry food. Some of them are loaded with albuminous granules. I have observed these wandering cells with acidophilic granules in some actinians.

Flatworms

Like the sponges, the flatworms have a parenchyma or mesenchyme which occupies the space between the dermal layer and the viscera. Simple forms like *Planaria* have no blood or lymph vessels but merely intercellular lacunae in the parenchyma; others have definite vascular channels, which represent intercellular lacunae walled off.

In the intercellular lacunae and in the vascular channels of those species in which vessels exist, one finds a variety of free cells. Among these are cells with a little basophil cytoplasm surrounding a vesicular nucleus with one or more nucleoli. Various workers (Prenant, '23, Jordan, '33) find these to be homocyto-

blasts and others (Curtis and Schulze, '34) find them to be totipotent cells. Other free cells, varying somewhat in types in different species, are found in the lacunae and blood vessels. A few species are said to have red cells that contain hemoglobin and there are amoeboid cells with acidophil granules and phagocytic cells containing ingested materials.

Although we have inadequate information relative to the part played by the mesenchyme in digestion in flatworms it seems certain that the phagocytic cells and perhaps the granular cells participate in the nutritive process. An enteron is present in most flatworms, but in simple forms like *Planaria* there is no digestion within the lumen. That the epithelium of the gut phagocytoses the food and digests it intracellularly has been known since Metschnikoff's (1880) observations. Later more detailed work has been done by Westblad ('23), Willier, Hyman and Rifenburgh ('25), Kelly ('31). In such forms as *Convoluta* and *Haplo-discus* belonging to the group of the Acoela, there is no gut lumen but a central nucleated mass of protoplasm, the syncytial hypoblast or "digesting parenchyma," in which remnants of prey are found. In *Proporus* and some other turbellarians the digesting parenchyma consists of separate amoeboid cells (Benham, '09a). According to a commonly accepted interpretation the Acoela are looked upon phylogenetically as being degenerate not primitive forms. If this interpretation is correct the presence of a digesting parenchyma is a derived, degenerate condition. However, there is some basis for looking upon them as primitive flatworms. This thesis is supported in an unpublished paper by M. A. Stirewalt.

Echinoderms

The echinoderms do not have a true vascular system but an extensive system of

lacunae and sinuses communicating with the body cavities and the exterior. The fluid in the body cavities and the lacunar system is similar except that the coelom is said to contain more sea water and correspondingly less dissolved albumen.

The cells found in the lacunae are identical with those in the coelomic cavities,—in fact they may wander from one location to the other and throughout all the tissues. The blood cells (coelomic corpuscles) of echinoderms have been described by Geddes (1880), Cuenot (1891), Saint-Hilaire (1898), Kollmann ('08), Théel ('20), Kindred ('21, '24, '26), and others. The structure of the different types of cells varies somewhat in different species, and some types are found in all species while others are of limited distribution.

The following cell types appear to be universally distributed within the phylum:

1) Leucocytes with nucleolate nuclei and petaloid or membranous pseudopodia. Goodrich ('19) first described the true nature of their pseudopodia. They have long been recognized as phagocytes: see Kindred ('24) who cites some of the earlier observations. They take up carmine and trypan blue, give a positive oxidase reaction (Ohuye, '36a, b), and contain small neutral red bodies or vacuoles. These cells are probably the echinoderm equivalent of the mammalian macrophage.

2) Cells with spherules, which may be colorless, red, green, yellow, or brown. The cells with colorless spherules are always present and one or more of the colorless types usually occur. Cuénot (1891) believes that these cells arise from cells of the preceding type through the addition of spherules of protein. Kindred ('26) believes that the various colored globules result from the partial digestion of colorless globules. That the various types of spherules differ somewhat in

nature as well as in color is shown by some of their reactions. For example, I have observed that the red spherules of some species (*Arbacia punctulata*, e.g.) are destroyed by weak HCl or by the acid of acidulated methyl green used for the nuclear staining of fresh cells, a reaction suggesting an albuminous composition of the spherules, and that they blacken with osmic acid, whereas the colorless spherules are more distinctly seen after the weak acid and they are negative to osmic acid. It seems probable that they are to be regarded as food carriers. They are neutral red positive and Ohuye ('36a, b) has reported a positive oxidase reaction for the colorless and for the brown globules. Saint-Hilaire (1898) and later workers find them to exist as migratory cells in the tissues, and especially in the wall of the intestine. Cannan ('27) finds that the red pigment in cells of the coelomic fluid and some other tissues of *Arbacia* function as an oxidation reduction system.

In the echinid *Temnopleurus* there are amoebocytes with fine granules that are positive to Best's carmine test for glyco-gen (Ohuye, '36b).

The following types of cells are of limited distribution:

3) Vesicular and compartment cells with brownian granules in the vacuoles. They are very similar in structure and reactions to cells that I have described elsewhere for tunicates, and they have been reported by various authors as occurring in annelids also. The granules stain with 1 to 8000 neutral red and with 1 to 40,000 Nile blue sulphate and Ohuye ('36b) reports a positive oxidase reaction.

4) Cells with long flagella called "vibratile cells." A few small neutral red granules are present in the cell bodies. In the absence of a heart in echinoderms, these vibratile cells, in conjunction with "ciliated cups" and "urns" and the

ciliated epithelium of the coelom, serve to keep the fluid agitated.

5) Red cells, or hemocytes, containing hemoglobin. Such cells are not found in all echinoderms but occur in those holothurians that have a considerable amount of highly contractile muscle and so require efficient oxygen and carbon dioxide exchange (Kindred, '24).

6) Lymphocytes or stem cells. These have not been generally recognized in previously published lists of echinoderm cells although Kollmann does speak of hyaline leucocytes of stage I. They are small spherical cells of the large lymphocyte or hemocytoblast type. In its simplest form the cell has a large vesicular nucleolate nucleus and a thin shell of cytoplasm devoid of neutral red or Nile blue staining granules. Cells interpreted as transitions show a few stainable granules. In the sand-dollar, *Enchope michelini*, such small spherical cells with vesicular nucleolate nuclei and transition stages as well as easily found in coverslip preparations of fresh coelomic fluid stained with neutral red or Nile blue sulphate. The nucleus is revealed after treatment with osmic acid or acidulated methyl green. In sections also I have found these cells in sinuses of the body wall. In the sand-dollars, *Mellita sexiesperforata* and *M. quinquesperforata*, in the sea urchins, *Arbacia punctulata*, and in some starfishes and holothurians I have found them less easily and in smaller numbers. In some echinoderms I have not been able to find them at all. Theoretically these cells should be number 1 in the group of universally distributed cells. I assume that such cells are always present in the animal although apparently not always as free cells in the circulating fluids. Perhaps in some species of echinoderms, as in the birds and mammals, the hemocytoblasts do not ordinarily leave their site of origin

in the connective tissues under normal physiological conditions.

The opinion that some of the blood cells of echinoderms have a nutritive function is supported by Cuénot (1891) and Kollmann (1908). Their opinion is based in the main upon the extensive occurrence of granules and spherules of fatty and albuminous nature in the cells. The further evidence of positive neutral red and oxidase reactions is confirmatory. Moreover, Van der Heyde and Oomen ('24) consider that fine particles of food are taken up by wandering phagocytes in asteroidea. Oomen ('26a, b) found free amoebocytes in the lumen of the gut and an abundance of them in the epithelium. He, therefore, considers that they play an important part in the absorption and transport of nutrient materials.

Certain observations on the distribution of enzymes are of significance in this connection. Van der Heyde ('22, '23a) and van der Heyde and Oomen ('24) find that the stomach and gut of echinoderms yield a weak proteolytic enzyme but no amylolytic enzymes. Van der Heyde ('23b) confirms Cohnheim's finding of an amylolytic action of echinoderm coelomic fluid, but he concludes from his experiments that this action is due to the consumption of carbohydrate by "blood" corpuscles and not to an enzyme free in the plasma. Weese ('26) finds protease and amylase in extracts of the digestive tract but no lipase. He expresses the opinion that the weak pepsin-like enzyme is perhaps contained in the tissues rather than secreted into the lumen.

Annelids

There is a variety of cells in the blood and coelomic fluid of annelids. The presence of cells of stem-cell type seems established. They have been recorded in many genera by a number of workers some

of whom follow: in acanthodrilids by Benham ('01), in *Ctenodrilus* by Galvagni ('05), in *Arenicola*, *Glycera* and sipunculids by Kollmann ('08), in Lumbricidae by Cameron ('32), in various polychaetes by Romieu ('23), in *Drawidia*, *Terebella*, *Thalassema* and *Gephyrea* by Ohuye ('34, '37a), in *Pheretima* by Kindred ('29) and Ohuye ('37c). Common features of these cells are hyaline basophil cytoplasm, in some cases said to be scanty but in others more abundant than in vertebrates, and a spherical, oval or bean shaped nucleus. In some cases nucleoli are said to be absent (Kindred, '29); in others present. Nucleoli have been recorded in Lumbricidae by Cameron ('32) and in some geophyrean worms by Ohuye ('37a). Romieu ('23) records the presence of both microlymphocytes and cells comparable to hemocytoblasts.

In certain cases hyaline leucocytes have been said to be phagocytic (Romieu, '23, pp. 245, 248, Ohuye, '34, Kindred, '29), but there is evidence that the phagocytes have differentiated beyond the stem cell type. Kollmann ('08) recognizes in *Arenicola* a "stage II" which he says is characterized by an increase in cytoplasm and highly developed amoeboid and phagocytic powers. Phagocytic cells of *Pheretima indica* show petaloid pseudopodia (Kindred, '29) similar to those of vertebrate macrophages, of phagocytic cells of echinoderms and amoeboid cells of various other forms. Camerons ('32) reports that all types of earthworm coelomic corpuscles (but not chloragogen cells) are phagocytic for such things as india ink and carmine, although the larger nongranular cells are most active; and only the large basophilic type of corpuscle phagocytoses foreign cells such as spermatozoa and red blood corpuscles.

In addition to the above blastic cells and phagocytic cells, the blood of anne-

lids has other types of cells. Some of them contain fine or coarse granules, which may be acidophilic or basophilic; others have larger spherules; still others are compartment or vesicular cells (linocytes) similar to those of ascidians and echinoderms. In some cases the inclusions are reported to blacken with osmic acid, stain with Sudan III, and give a positive Millon test and so they are considered to be composed largely of fats and proteins. Very commonly they stain with neutral red, and in some cases they have been reported to give a positive oxidase reaction (Ohuye, '37a); in other cases the granules are said to be oxidase negative (Cameron, '32). Romieu ('23) finds that the leucocytes of polychaetes produce diastases. With regard to the chloragogen cells Cameron ('32) believes that "the fact that they are usually in the process of disintegration, liberating their characteristic granules of lipoid and protein, points in the direction of a metabolic function rather than protective." Conclusive evidence of the participation of the blood and coelomic cells of annelids in nutrition is lacking but the probability that some of the specialized cells have such a function should be considered.

Some species of annelids (*Glycera*, *Thalassema*, e.g.) have cells with respiratory pigments, and sometimes cells are present that are said to have an excretory function.

Brachiopods

Ohuye ('36b, '37b) reports concerning the blood of three genera of brachiopods (*Coptothyris grayi*, *Terebrataria coreanica*, and *Lingula unguis*). His analysis of the cells that he calls hyaline amoebocytes (5-12 μ in diameter) does not make it clear, but probable, that there are primitive spherical cells with a nucleolate nucleus surrounded by a little clear cytoplasm and also larger phagocytic cells

with more cytoplasm and probably without a nucleolus. Two of Ohuye's figures show a considerable amount of cytoplasm around the nucleus of these cells; one shows little. He states that the nucleus shows a nucleolus in the majority of cases. In his figures of the hyaline cells of *Lingula* the smaller cells are the ones that show nucleoli.

Ohuye reports other cells with granules of various sorts. Their reactions with osmic acid indicate the presence of fat in the inclusions. Intracellular enzyme activity is indicated by positive neutral red staining and oxidase reactions of the granules. That these cells are probably involved in the digestive processes of the organism is indicated by their inclusions and reactions. Furthermore, Yonge ('37, p. 89) states that there is probably no secretion and hence no digestion in the gut of *Lingula*.

Molluscs

In the lamellibranchs, the group of the molluscs in which the vascular conditions are perhaps best known, the blood is pumped from the heart through a system of more or less dilated vessels and sinuses with connective tissue walls but without an endothelium. In these vessels there are to be found the following types of cells (Cuenot, 1891, Bruyne, 1895, Kollmann, '08, Takatsuki, '34, and others):

- 1) Small cells with large nuclei and a little hyaline cytoplasm.
- 2) Phagocytic cells with more cytoplasm than the preceding.
- 3) Cells with granules in the cytoplasm. (Cells with large spherules are found in the connective tissue.)

The suggestion was made by some of the earlier investigators that the cells are involved in nutrition. Other workers seem to have shown conclusively that they have an important rôle in the nutri-

tion of the lamellibranchs. Outwandering phagocytes were recognized in the oyster, anodon and other lamellibranchs as long ago as 1893 by Lankester. I have observed them with ingested diatoms in the lumen of the gut. The excellent work of Yonge ('26, '28, '36) has given us considerable detailed information about these cells. He observed the actual digestion of olive oil emulsion and elasmobranch blood corpuscles by oyster phagocytes. Takatsuki ('34) found that the oyster amoebocytes possess sucroclastic, lipoclastic, and proteoclastic enzymes and that they are capable of absorbing glucose. He reports, furthermore, that amoebocytes play an important part in excretion, disposing of foreign indigestible matter by way of the excretory organ, pericardium, surface of the auricle, rectum, and mantle cavity.

Kollmann ('08, p. 65) reports that the granulations in cells of some Unios are much less numerous at the beginning of spring than at the end of autumn, and concludes that they are reserve nutriment. He states that the granular leucocytes so prominent in the lamellibranchs, are not found in the gastropods. The absence of these granular leucocytes in gastropods may bear some relation to the fact that digestion of proteins is extensive in the lumen of the gut of gastropods whereas it is very limited in the gut of lamellibranchs. Yonge ('37) states that throughout the gastropods there is a tendency for intracellular to be replaced by extracellular digestion, but that in certain genera absorption and all digestion of proteins and fats takes place within cells of digestive diverticula. In these genera there are no wandering phagocytes.

Arthropods

The conditions and homologies in the blood of crustaceans and some other arthropods are not yet clear enough to me

to justify me in attempting any analysis or generalizations. For data and references to the literature, the interested reader is referred to Kollmann ('08), Tait and Gunn ('20), and Maluf ('39).

Insects

In a recent valuable review with bibliography Mellanby ('39) points out that the blood cells of insects seem to be homologous to vertebrate leucocytes; none are respiratory in function. The corpuscles give the appearance of many different forms, but Mellanby thinks it possible that there is only one type of corpuscle with a different appearance at different stages in its development. He recognizes immature cells (free undifferentiated mesenchyme cells), basophil phagocytes, and eosinophilic non-phagocytic oenocytes of unknown function. The phagocytes, or perhaps the undifferentiated mesenchyme cells, take some part in producing internal membranes, and the phagocytes are important agents in breaking down obsolescent tissues, especially during the pupal period, which they digest and then set free their constituents to be reconstituted into other tissue. They also serve to protect the insect's body against invasion by foreign organisms, which they may ingest or encapsulate.

Ascidians

In ascidians the blood is pumped out from the tubular heart through main vascular channels into the sinuses and tissue spaces of the body. There is no distinction into blood, lymph, and tissue spaces. In the circulating fluid there are certain fundamental types of cells that are of universal occurrence; other cell types with very special functions are found in some species, not in others. Lymphocytes (or lymphoid hemoblasts), phagocytic cells, and cells with vacuoles

that contain inclusions of nutrient materials are present in all species; cells with carotinoid inclusions, nephrocytes, morula cells, and cells with fibrous inclusions have a limited distribution.

The lymphocytes are small, spherical cells with large, pale, nucleolate nuclei surrounded by a small amount of basophil cytoplasm that contains few or no neutral red granules or vacuoles. These cells are hemocytoblasts and transitions connect them with the more specialized cell types. A number of workers (Brien, '30; Devinney; '34, Berrill, '35) find them to be the cells which give rise to all the organs of new individuals in budding and regeneration.

Macrophages have more abundant cytoplasm surrounding the nuclei, which in older stages have lost the nucleoli. The cytoplasm contains neutral red staining vacuoles in which ingested materials are frequently found.

The cells with nutrient inclusions are of a variety of sorts. They have smaller nuclei than the preceding types of cells, and the cell bodies contain large or small vacuoles with fluid or granular inclusions that stain with neutral red and with various other dyes. The nature of the fluid and the inclusions in the vacuoles giving the neutral red reaction, supported by the fact that a positive oxidase reaction has been reported in some of these cells, gives basis for interpreting the reactions that go on within the vacuoles as being hydrolytic or synthetic (or both) chemical changes. In this connection it is worthy of note that Yonge ('25) and Berrill ('29) find in some species of ascidians that the enzymes of the gut lumen are weak and do not complete the splitting of the proteins of the food into amino acids. Furthermore, Henze ('12) corroborates the earlier observation of Krukenberg that the plasma of ascidians is poor in dissolved albumens. These

facts have led me to assume that the incompletely hydrolyzed foods diffuse through the wall of the intestine into the vascular lacunae and are taken up into the vacuoles of the blood cells where chemical changes are continued to the point where the nutrient materials are utilizable by those tissues that have little digestive capacity.

There is some histological evidence to support the above view. In the wall of the gut the blood circulates in broad lacunae and comes into direct contact, to a greater or less extent in different species, with the bases of the epithelial cells. It seems that this arrangement would facilitate the passage of materials from the lumen of the gut into the lacunae and absorption by the blood cells. The blood cells subsequently wander freely through the tissues, and sections show blood cells applied to the fixed tissues (muscles, etc.) as if they were serving as nurse cells to these tissues. In fact, many of them are virtually identical in structure with the nurse cells surrounding eggs, and the inclusions of the two are histologically similar. (For further details and bibliographies concerning the blood of ascidians see George ('39) and Webb ('39).)

Vertebrates

In the vertebrates, red cells, which are present in some invertebrates but absent in most, have become the dominant cells—a dominance correlated with differences in respiratory conditions and requirements. On the other hand leucocytes constitute a relatively small proportion of the cells present in vertebrates whereas they are the dominant cells or the only cells present in the circulating blood and body fluids of invertebrates. Are the leucocytes of vertebrates comparable to those of invertebrates, and with what difference in

physiological conditions may their relatively minor proportion be correlated?

It appears that in the vertebrates, including the mammals, there are free cells as well as fixed cells of embryonic potencies comparable to the blastic cells (lymphocytes and fixed mesenchyme cells) of the invertebrates; there are phagocytic cells of limited developmental potencies; and there are granular leucocytes. In the higher vertebrates lymphocytes, lymphoblasts, and hemocytoblasts are recognized, although neither the lymphoblasts nor the morphologically and probably functionally equivalent hemocytoblasts are normally found in the blood stream. They exist as free cells in the lymphoid tissue and bone marrow, and probably are equivalent to fixed mesenchyme cells of the connective tissues. There is much evidence to indicate that the lymphocytes of the blood and lymph channels have potentialities similar to the lymphoblasts, hemocytoblasts, and fixed mesenchyme cells (see Bloom, '37; and other authors), although students of vertebrate blood are not in agreement upon this point.

The vertebrate monocytes and macrophages appear to be comparable though not necessarily identical in structure and functions to the phagocytic cells of the invertebrates. They assist in disposing of foreign bodies and senile or necrotic tissues of the organism and perform other functions. Lewis ('37) has observed that they have membranous processes similar to those of the phagocytic leucocytes of echinoderms and other groups and that these membranous pseudopodia play an important part in the drinking in of body fluids by the cells. Lewis believes that these cells exercise a digesting, modifying action on the body fluids.

Are the granular leucocytes likewise comparable to those invertebrate granular leucocytes to which I have attributed a

primarily nutritive function? Their granules are correspondingly neutral red positive and oxidase positive. Furthermore, leucocytes of the vertebrates have been shown to have the power of digesting substances, and various enzymes have been obtained from them (Opie, '22; Willstätter and Rhodewald, '31; Stern, '32).

The reactions of vertebrate blood cells to nutrient materials is significant also. Clark and Clark ('17) demonstrated that experimentally introduced fatty materials incite active migration of leucocytes from blood vessels into extra-vascular tissue, and Emmel, Weatherford, and Stricher ('26) find that there is a passage of leucocytes into the alveoli and ducts of the mammary gland throughout the period of lactation. The increase in the number of leucocytes in areas of inflammation or around endogenous or exogenous dead material or throughout the whole body in certain pathological conditions in which there is abnormal tissue disintegration might be explained as a response of the cells to an increased abundance of undigested materials. Furthermore, it is common knowledge that large numbers of leucocytes, especially lymphocytes, pass through the epithelium of the gut into its lumen. It is not known what significance there is in this phenomenon, but it seems likely that it is a response of cells to nutrient materials. We have seen that a similar phenomenon has a great deal of functional significance in sponges and oysters and, perhaps, in some other forms in which digestion takes place largely intracellularly in the leucocytes. In the vertebrates in which digestion takes place largely extracellularly in the lumen of the gut it may be a persisting reaction without any great physiological usefulness.

Clinicians have observed a close relationship between disturbances of the gastro-intestinal tract and anemias, and, fur-

thermore, there is experimental evidence to show that nutrient materials have a pronounced effect on the production of various types of blood cells. Settles ('20) finds in kittens that a high fat, high calorie diet produces a general enlargement of the lymphoid tissue of the body. Also at the 1938 meetings of the American Association of Anatomists, Prof. C. M. Jackson reported a very great loss of weight in the thymus and other lymphoid organs of rats kept on an inadequate diet and a rapid seven-fold increase in this tissue when the animals were restored to a full diet. Wiseman, Doan, and Erf ('36) find that foreign proteins injected into the body are important factors affecting the production of both lymphocytes and granular leucocytes. Jordan ('38) obtained interesting results from starving salamanders for some weeks. He finds that the leucocytes are greatly reduced in number; the eosinophils completely disappear; the neutrophils and basophils lose their granules; the production of granulocytes in the liver ceases. After two weeks of adequate feeding there is complete restoration of normal conditions. It is interesting to note that Kollmann ('08) made comparable observations on crabs many years ago. He reports that in these animals the granules in the blood cells become greatly reduced in number during the molting period, during which time the animals do not feed. These observations seem to show that scarcity of nutrient materials in the body fluids causes an alteration in the structure and a reduction in the number of leucocytes and an atrophy of the lymphopoietic tissue; abundance of nutrient materials causes an increase in the number of granules and granular leucocytes and an hypertrophy of the blood-forming tissue up to a certain level.

Further evidence in support of the hypothesis of a primitive nutritive signifi-

cance of blood is found in the fact that in both the ontogeny and phylogeny of vertebrates blood formation is intimately associated with the digestive tract. The first blood in the embryo is formed in the mesoderm of the yolk sac adjacent to the food-bearing endoderm. Subsequently blood is formed in the liver, which is of gut tract origin and of nutritive significance, and in the spleen and other hemopoietic regions of the gut tract. It is only in the higher vertebrates that the bone marrow takes over the principal blood-forming function, and even in these forms the wall of the gut remains one of the important areas of leucocyte production throughout life. Furthermore, it seems significant that the anti-pernicious anemia principle influencing erythrocyte production originates in the stomach. In the phylogeny of vertebrate hemopoietic tissue it seems evident that the primitive blood-forming tissue is the mesodermal envelope of the enteron. In the hagfish this tissue is diffusely scattered throughout the length of the gastrointestinal tract, but as we ascend the scale of the vertebrates we find special loci of hemogenesis developed (Jordan, '33).

Despite the evidence that I have cited to support the thesis of a primary relationship of the leucocytes to the processes of digestion and nutrition in animals generally, it seems unlikely that the leucocytes normally play a very important part in these processes in mammals or other vertebrates. In the absence of a digestive tract in sponges, other tissues must do the job of splitting the complex proteins, carbohydrates, and fats of the food into simpler molecules that the tissues of the organism can use to do work and build up their own protoplasm. In the sponges and some of the flatworms it has been seen that the parenchyma, the blood homolog, carries out this function. In the ascidians the digestive tract has be-

come an effective digesting organ, but even here it appears that digestion is not completed in the lumen of the gut and the final phases are probably left for the blood cells. Among the vertebrates the epithelium of the gut tract and of the glands derived from it has developed a very efficient enzyme secreting function and the gut has taken over one of the major primitive functions of blood. Nevertheless, it may be that physiological leucocytosis of digestion and pregnancy should be looked upon as a primitive response of the blood forming tissues to an excess of foreign substances of nutritive value. Under pathological conditions the leucocytes come into function in the digestion of dead and dying tissue. So far as their primitive function is concerned it seems that the granular leucocytes of vertebrates may be looked upon as surviving cells that have been largely out moded in the process of evolution. In a sense then they are vestigial. It may be, however, that the leucocytes have taken over certain special metabolic processes related in nature to their original function. For example, the formation of bile pigments, formerly credited to the liver cells, is now recognized as a function of the reticulo-endothelial cells (see Lemberg, '38), and one may hazard the suggestion that the leucocytes play a part in the formation of plasma proteins. There is some support for this suggestion in the hyperproteinemia observed in myeloid leucemia (see Luck, '38).

SUMMARY

The vertebrates and most of the invertebrates have free cells of mesenchymatous

origin. In some groups these cells are more or less confined to vascular and lymphatic vessels; in others they wander through the tissue spaces. In all groups that have been satisfactorily investigated certain fundamental types of cells are found:

- 1) Relatively undifferentiated cells that have the capacity to differentiate into other types of blood cells or wandering cells, and, in some groups and possibly in all, into any type of cell in the body including the genital cells.

- 2) Phagocytic cells that serve the function of consuming foreign materials and dead or damaged tissue of the animal itself.

- 3) A greater or smaller number of various types of more specialized granular and vacuolated cells that contain nutritive materials and give evidence of enzyme activity. In many low forms these constitute an important part of the food handling and digesting mechanism. In other forms, including the vertebrates, their original function has been taken over largely by the digestive glands of the gut tract.

Of limited distribution, present in animals of some groups but not in others, are specialized cells of a variety of types serving other special functions characteristic for the animals in which they are found. To be included here are such cells as the cells with respiratory pigments found in the vertebrates and some invertebrates with high oxygen requirements; the carotene bearing cells and the excretory cells of some ascidians; and the flagellate cells of some echinoderms which, in the absence of a heart, keep the fluid in circulation.

LIST OF LITERATURE

- BERRILL, N. J. 1929. Digestion in ascidians. *Brit. Jour. Exp. Biol.*, 6: 275-292.
- . 1935. Studies in tunicate development. IV. Asexual reproduction. *Phil. Trans. Roy. Soc. Lond.*, B, 225: 327-379.
- BLOOM, WILLIAM. 1937. Transformation of lymphocytes into granulocytes *in vitro*. *Anat. Rec.*, 69: 99-121.
- BENHAM, W. B. 1901a. The Platyhelminia, Mesozoa and Nemertini. In Lankester's Treatise on Zoology, pt. IV: 1-204.
- . 1901b. The coelomic fluid in Acanthodrilids. *Quart. Jour. Micr. Sci., N.S.*, 44: 565-590.
- BOCHMA, H. 1925. On the feeding reactions and digestion in the coral polyp. *Biol. Bull.*, 49: 407-439.
- BRAEM, F. 1908. Die Knospung der Margeliden, ein Bindeglied zwischen geschlechtlicher und ungeschlechtlicher Fortpflanzung. *Biol. Centralblatt*, 28: 790-798.
- BRIEN, P. 1930. Contribution à l'étude de la régénération naturelle et expérimentelle chez les Clavelinidae. *Ann. Soc. Roy. Zool. Belgique*, 61: 19-112.
- BRUYNE, C. DE. 1895. Contribution à l'étude de la phagocytose. *Arch. Biol.*, 14: 161-241.
- CAMERON, G. R. 1932. Inflammation in Earthworms. *J. Path. and Bact.*, 35: 933-972.
- CANNAN, R. K. 1927. Echinochrome. *Biochem. Jour.*, 21: 184-189.
- COTTE, J. 1904. Contribution à l'étude de la nutrition chez les spongiaires. *Bull. Sci. France-Belg.*, 38: 420-573.
- CLARK, E. R., and E. L. CLARK. 1917. A study of the reaction of lymphatic endothelium and of leucocytes, in the tadpole's tail, towards injected fat. *Am. Jour. Anat.*, 21: 421-448.
- CUÉNOT, L. 1891. Études sur le sang et les glandes lymphatiques dans la série animale. *Arch. Zool. Exp. et Gén.*, 2me Serie, 9: 13-90.
- CURTIS, W. C., and L. M. SCHULZE. 1934. Studies upon regeneration. *Jour. Morph.*, 55: 477-513.
- DEVINNEY, E. M. 1934. The behavior of isolated pieces of ascidian (*Perophora viridis*) stolon as compared with ordinary budding. *Jour. Elsie Mitchell Sc. Soc.*, 49: 185-224.
- DURHAM, H. E. 1891. On wandering cells in echinoderms. *Quart. Jour. Micr. Sci., N.S.*, 33: 81-121.
- EMMEL, V. E., H. L. WEATHERFORD, and M. H. STREICHER. 1926. Leucocytes and lactation. *Am. Jour. Anat.*, 38: 1-39.
- GALVAONI, E. 1905. *Ctenodrilus*, histologische Untersuchung des Genus. *Arch. zool. Inst. Wien.*, 15: 47-81.
- GEDDES, P. 1880. Observations sur le fluide périsvical des oursins. *Arch. zool. exp. et gén.*, 1re série, 8: 483-496.
- GEORGE, W. C. 1939. A comparative study of the blood of tunicates. *Quart. Jour. Micr. Sci., N.S.*, 81: 391-428.
- GOODRICH, E. S. 1919. The pseudopodia of the leucocytes of invertebrates. *Quart. Jour. Micr. Sci., N.S.*, 64: 19-26.
- HARGITT, G. T. 1916. Germ cells of coelenterates. *Jour. Morph.*, 27: 85-97.
- HENZE, M. 1912. Untersuchungen über das Blut der Ascidien. II. *Zeitschr. Physiol. Chem.*, 79: 215-228.
- HEYDE, H. C. VAN DER. 1922. On the physiology of digestion, respiration and excretion in echinoderms. Academic Thesis, Amsterdam.
- . 1923a. La résorption chez les échinoderms. *Arch. Neerl. Physiol.*, 8: 118-147.
- . 1923b. Y-a-t-il des enzymes dans le liquide périsvical des échinoderms? *Ibid.*, 8: 148-150.
- , et H. A. P. C. OOMEN. 1924. Sur l'existence chez les étoiles de la mer d'une digestion intracellulaire. *Arch. Intern. Physiol.*, 24: 41-53.
- KELLY, E. G. 1931. The intracellular digestion of thymus nucleoprotein in triclad flatworms. *Physiol. Zool.*, 4: 515-541.
- JORDAN, H. E. 1933. The evolution of the blood-forming tissues. *QUART. REV. BIOL.*, 8: 58-76.
- . 1938. Blood-cell changes during experimental nutritional deficiency anemia and recovery in the newt, *Triturus viridescens*, with special reference to the erythrocytes. *Jour. Morph.*, 63: 143-161.
- , and D. B. REYNOLDS. 1933. The blood cells of the trematode *Diplodiscus temperatus*. *Jour. Morph.*, 55: 119-129.
- KINDRED, J. E. 1921. Phagocytosis and clotting in the perivisceral fluid of *Arbacia*. *Biol. Bull.*, 41: 144-152.
- . 1924. The cellular elements in the perivisceral fluid of echinoderms. *Ibid.*, 46: 228-251.
- . 1926. A study of the genetic relationships of the "amoebocytes with spherules" in *Arbacia*. *Ibid.*, 50: 147-154.
- . 1929. The leucocytes and leucocytopoietic organs of an oligochaete, *Pheretima indica* (Hort). *Jour. Morph.*, 47: 435-478.
- KOHRING, VERA. 1930. The neutral red reaction. *Jour. Morph.*, 49: 45-137.

- KOLLMANN, M. 1908. Recherches sur les leucocytes et le tissu lymphoïde des invertébrés. Thesis, Paris. *Ann. Sc. Nat. Zool., Ser. 9*, 8: 1-230.
- LEMBERG, R. 1938. The disintegration of haemoglobin in the animal body. In *Perspectives in Biochemistry*, 137-149. Cambridge Univ. Press.
- LENDENFELD, R. V. 1890. Experimentelle Untersuchungen über die Physiologie der Spongien. *Biol. Centralbl.*, 10: 71-110.
- LEWIS, W. H. 1937. Pinocytosis—drinking by cells. *Science*, 85: 437.
- LUCK, J. M. 1938. The liver proteins. In *Perspectives in Biochemistry*, 215-229. Cambridge Univ. Press.
- MELLANBY, K. 1939. The functions of insect blood. *Biol. Rev.*, 14: 243-260.
- METSCHNIKOFF, E. 1880. Über die intracelluläre Verdauung bei Coelenteraten. *Zool. Anz.* 3: 261-263.
- MINCHIN, E. A. 1900. Sponges. In *Lankester's Treatise on Zoology*, Pt. II, chap. 3: 1-178.
- ORUYE, T. 1934. On the coelomic corpuscles in the body fluid of some invertebrates. II. On the coelomic corpuscles of an earthworm, *Drawidia battanimitzu* Hatai. *Sci. Rep. Tōhoku Imp. Univ., Biol.*, 9: 53-60.
- . 1936a, IV. On the coelomic corpuscles of a holothurid. . . *Ibid.*, 9: 207-222.
- . 1936b, V. Reaction of the coelomic corpuscles of an echinid, *Temnopleurus hardwicksi* (Gray), to vital dyes and some chemical reagents. *Ibid.*, 11: 223-230.
- . 1936c, VI. A note on the formed elements in the coelomic fluid of a brachiopod, *Terebratalia coreanica*. *Ibid.*, 11: 231-239.
- . 1937a, VII. On the formed elements in the body fluid of some marine invertebrates which possess the red blood corpuscles. *Ibid.*, 12: 203-239.
- . 1937b, VIII. Supplementary note on the formed elements in the coelomic fluid of some Brachiopoda. *Ibid.*, 12: 241-253.
- . 1937c, IX. On the coelomic corpuscles of an earthworm, *Pheretima sieboldi* Horst. *Ibid.*, 12: 255-263.
- OOMEN, H. A. P. C. 1926a. Verdauungsphysiologische studien an Holothuriern. *Publ. Sta. Zool. Napoli*, 7: 215-298.
- . 1926b. On the permeability of the gut in sea cucumbers. *K. Akad. Wetenschap. Amsterdam. Proc. Sect. Sci.* 29: 1000-1007.
- OPIE, E. L. 1922. Intracellular digestion. *Physiol. Rev.*, 2: 552-585.
- PENNY, J. T. 1933. Reduction and regeneration in fresh water sponges (*Spongilla discoides*). *Jour. Exp. Zool.*, 65: 475-497.
- PRAATT, E. M. 1906. The digestive organs of the Alcyonaria and their relationships to the mesogloecal cell plexus. *Quart. Jour. Micro. Sci.*, 49: 327-362.
- PRENANT, M. 1922. Recherches sur le parenchyme des platyhelminthes. *Arch. de Morph. gén. et exp.*, 5: 1-174.
- RINGOEN, A. R. 1923. The mast leucocytes in the adult guinea pig under experimental conditions. *Am. Jour. Anat.*, 31: 319-338.
- ROMIEU, M. 1923. Recherches histologiques sur le sang et sur le corps cardiaque des annélides polychètes. *Arch. Morph. gén. et exp.*, 17: 1-339.
- RUNNSTRÖM, J. 1929. Zur Kenntnis der Histophysiologie von *Clava squamata* (O. F. Müller). *Acta Zoologica*, 10: 1-58.
- SAINT-HILAIRE, C. 1897. Über die Wanderzellen in der Darmwand der Seeigel. *Trav. Soc. imp. Saint-Petersbourg*, 27: 221-248 (résumé).
- SETTLES, E. L. 1920. The effect of high fat diet upon the growth of lymphoid tissue. *Anat. Rec.*, 20: 61-93.
- SMITH, H. G. 1937. Contributions to the anatomy and physiology of *Cassiopa frondosa*. *Tortugas Lab. Papers*, 31: 19-52.
- STERN, K. G. 1932. Über die Katalase farbloser Blutzellen. *Zeitschr. f. Physiol. Chem.*, 204: 259-282.
- TAKATUKI, S. 1934. On the nature and function of the amoebocytes of *Ostrea edulis*. *Quart. Jour. Micro. Sci.*, 74: 379-431.
- THÉEL, H. 1920. On the amoebocytes and other coelomic corpuscles of the perivisceral cavity of echinoderms. III. Holothurids. *Arkiv. für Zool.*, 13, 25: 1-40.
- TRIOT, H. VAN. 1919. A contribution to the physiology of the fresh-water sponges. *Tijds. Neder Dierk. Vereen.* (2), 17: 1-220.
- WEBB, D. A. 1939. Observations on the blood of certain ascidians, with special reference to the biochemistry of *Vanadium*. *Jour. Exp. Biol.*, 16: 499-523.
- WEBER, A. O. 1926. The food and digestive processes of *Strongylocentrotus drobachianus*. *Publ. Puget Sound Biol. Station*, 5: 165-179.
- WESTBLAD, E. 1923. Zur Physiologie Turbellarien. *Lunds Univ. Arsskr.*, N.F., A.vd. 2, 18; Nr. 6: 1-212.

- WILLEY, C. H. 1930. Studies on the lymph system of digenetic trematodes. *Jour. Morph.*, 50: 1-37.
- WILLIERS, B. H., L. H. HYMAN, and S. A. RIVENBURGH. 1925. A histochemical study of intracellular digestion in triclad flatworms. *Ibid.*, 40: 299-340.
- WILSON, H. V. 1935. Some critical points in the metamorphosis of the halichondrine sponge larva. *Ibid.*, 58: 285-353.
- , and J. T. PENNY. 1930. The regeneration of sponges (*Microciona*) from dissociated cells. *Jour. Exp. Zool.*, 56: 73-147.
- WISEMAN, B. K., C. A. DOAN, and L. A. ERF. 1936. A fundamental reciprocal relationship between myeloid and lymphoid tissues. *Jour. Am. Med. Assn.*, 106: 609-614.
- WILSTÄTTER, R., and M. ROHDENWALD. 1931. Über Desmo- und Lyo-trypsine der farblosen Blutkörperchen. *Zeitschr. f. Physiol. Chem.*, 204: 181-196.
- YONGE, C. M. 1925. Secretion, digestion and assimilation in the gut of *Ciona intestinalis*. *Brit. Jour. Exp. Biol.*, 2: 373-388.
- . 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. *Jour. Marine Biol. Assn.*, 14: 295-386.
- . 1928. The absorption of glucose by *Ostrea edulis*. *Ibid.*, 15: 643-653.
- . 1930. II. Digestive enzymes. *Sci. Reports G. Barrier Reef. Exped., Brit. Mus. (Nat. Hist.)*, 1: 283-322.
- . 1931. Digestive processes in marine invertebrates and fishes. *Jour. du Cons. Internat. pour l'Explor. de la Mer*, 6: 175-212.
- . 1936. Mode of life, feeding, digestion and symbiosis with zooxanthellae in Tridacnidae. *Sci. Rep. Great Barrier Reef. Exped., Brit. Mus. (Nat. Hist.)*, 1: 283-322.
- . 1937. Evolution and adaptation in the digestive system of the metazoa. *Biol. Reviews*, 12: 87-115.





THE LABORATORY POPULATION AS A TEST OF A COMPREHENSIVE ECOLOGICAL SYSTEM (*Concluded*)

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Aggregation and Coaction

EARLIER in this paper the point was made that aggregation occurs in nature, and, as a result, coactions are set up. These coactions are designated in terms of their end-effect on the population as co-operation, disoperation, and competition. It is our plan to illustrate these three forms of coaction by the data of experimental population studies. One clarification is necessary before proceeding. We shall be discussing *Tribolium* and *Drosophila*. Populations of these species are aggregations in the statistical sense that they are groups of organisms, and in the biological sense that they respond as a unit or population integrated by biological processes. They are not, however, as closely-knit aggregations as can be studied under laboratory conditions. Laboratory aggregations often occur without physical crowding within a habitat. This means that their reality as aggregations does not depend on spatial confinement. A few examples of the latter follow: aggregations of *Paramecium*, terrestrial isopods, schooling fish, all truly social insects, *Asellus* (isopod) and certain amphipods during the breeding season, many birds under night roosting conditions, earthworms when the soil loses moisture, tubifex worms, mice at night or when the temperature lowers,

and so on. These aggregations also furnish interesting material for coaction analyses. They can not be studied here but the writings of Allee (1931; 1934; 1938) should be consulted for further information.

Co-operation

Tribolium. Chapman (1928) in his stimulating paper on biotic potential incidentally published some data that furnished the impetus for a study of co-operative coaction during the early growth of *Tribolium* populations. These data are reproduced in Table 6. Their reproductive performance in beetle cultures started at different population densities is summarized. Among other things, the table shows that at the first two censuses, 11 and 25 days, a population of intermediate size (two pairs of beetles in 32 grams of flour or 0.125 beetles per gram) produced more progeny per female than smaller or larger cultures. The significance of this point was neglected by Chapman but stressed by Allee (1931, p. 179) as another possible illustration of "undercrowding." An undercrowding effect exists when, for any biological process, the maximum response consistently occurs, not in the population of least possible density, but in a somewhat more crowded culture. When such an effect is shown, either for

natural or laboratory populations, to be due primarily to coaction then co-operation in the sense of Clements and Shelford has been demonstrated. By focusing attention on Chapman's protocol Allee stimulated MacLagan (1932) and Park (1932, 1933) to test this phenomenon independently. These two studies showed that the effect suggested in Chapman's original paper could be reduplicated. In other words, two pairs of *Tribolium* in 32 grams of flour produced significantly more eggs per female at the time of the first egg census than did smaller (1 pair) or larger (4, 8, 16, 32 pairs) populations.

With the reality of the effect established, an analysis of causal factors was under-

cannibalism. This reduced population growth rate in more crowded cultures since more eggs would be found by random moving beetles and eaten. The factor then favors greatest increase in minimal sized groups. The second factor was the question of frequency of copulations. It was found that recopulation was stimulating to reproductive productivity and since more copulations were occurring in concentrated populations this fact favored greatest increase in maximal sized groups. The interaction of these factors, one favoring maximal growth in small populations and the other favoring maximal growth in large populations, would cause an intermediate sized population to have greatest initial increase."

Let us examine this initial population effect as an illustration of Clements' and Shelford's co-operative coaction. Two questions immediately arise: (1) to what extent is this effect really co-operation,

TABLE 6

Data of Chapman (1928) recalculated to emphasize the initial optimal population effect

Volume of medium (gm.)	32	32	32	32	32	32
Imagoes (pairs)	1	2	4	8	16	32
Beetles per gram	0.026	0.125	0.25	0.5	1.0	2.0
Progeny per imago per day	1.59	3.90	3.18	2.82	2.36	1.82

taken. Here, MacLagan and Park reached different conclusions. The former suggested that at the optimal density a "sensitisation" (p. 443) of the organisms took place; probably through some psychological mechanism. In a later paper MacLagan and Dunn (1936) worked with a weevil, *Sitophilus oryzae*, and concluded that, "... living organisms are not always the highly coordinated physiological units they are often represented to be ... and some should be regarded as heterogeneous assemblages of diverse physiological processes, each with its own optimum, rather than harmonious physiological units" (p. 136).

Park (1933, p. 40) suggested a different type of explanation for the observed optimum density effect. He said,

"This [effect] was found to be due to the interaction of two factors. The first factor was egg eating, or

and (2) what are the major coactions involved? Turning to the first question it appears that the effect is co-operative, i.e. of benefit to the population, from a short-time viewpoint only. It has been shown that certain *Tribolium* populations of intermediate density have a higher productivity *per adult beetle* during their early history than larger or smaller cultures. This may be of some value in aiding these populations to get established and from this point of view the effect can be called co-operative. However, Chapman (1928) showed that all *Tribolium* cultures eventually reached a similar numerical equilibrium in terms of beetles per gram of medium (43.97 ± 2.88 for his culture conditions) that was independent of the initial density conditions. This means that the early optimal effect may be

of no permanent importance in the total population life-history.

The effect is worthy of analysis, however, because (1) it illustrates in the laboratory a type of response that is frequently of real significance in the establishment of field communities, and (2) it focuses attention on a series of coactions that are important in the integration of *Tribolium* populations. The analysis of Park summarized above shows that the optimal population effect results more from the secondary or coaction cycle than from the primary or action-reaction cycle. The important coactions are egg-eating and copulation frequency. Egg eating occurs in direct proportion to imago density and egg density. When taken by itself, this co-action is really a good example of competition since the beetles compete for a limited supply of eggs. However, in conjunction with copulation it results in the co-operative end-effect noted. The copulation coaction is based on the beetles' sexual behavior; namely, random movement with copulations a frequent result of the meeting of males and females. Thus, up to a point, copulation frequency is also in direct ratio to imago density. The population significance of this coaction lies in its stimulatory effect, again within limits, upon the fecundity of female *Tribolium*. We must recognize that the importance of these copulation and recopulation effects is not limited to the initial populations; this is a coaction that is probably essential in all *Tribolium* cultures.

Before passing on to *Drosophila* another brief example of co-operation in *Tribolium* populations should be noted. The beetles (imagos and larvae) are continually moving through their flour. In certain kinds of flour this movement is difficult for newly established cultures because there are no tunnels. The early members

of a culture prepare the medium through their own activity for the use of forms to come by creating such passageways. This statement should not be construed as teleological. While the significance of this effect has not been investigated, it seems safe to guess that it is of enough influence to warrant notice. It will be recalled that this effect was mentioned under reaction. It was properly introduced there and properly included here. The reaction is, obviously, the alteration imposed on the habitat. The coaction is based on the fact that all the beetles move, and move with reference to each other through the flour.

Drosophila. One of the most striking laboratory demonstrations of co-operation has been reported by Pearl, Miner and Parker (1927) in their studies on the effect of imago population density on the duration of adult life in *Drosophila*. As we shall see the conclusions reached in this investigation are clear although the causal factors unfortunately have not been analyzed. The experiments are particularly important in the population sense because they deal with mortality. The basic data are presented in abbreviated form in Table 7 and are well summarized by Hammond (1939) who says,

"... the flies, just a few hours old, were placed in one-ounce glass vials with banana-agar medium seeded with a standard amount of yeast. The vials were closed with cotton plugs permitting circulation of air. Each day the flies were changed to a new vial and any dead flies counted (but not replaced.) Two, 4, 6, 8, . . . 125, 150 and 200 flies (20 steps in all) were initially placed in each vial, there being a total of 530 vials and 13,000 flies in all. As was to be expected, the higher densities considerably shortened the duration of life but the more significant point was that up to a density of between 30 and 55 flies per vial at the start *increasing density significantly prolonged the duration of life*. . . Further studies showed that densities above 200 flies per bottle at the start had little further effect in reducing the duration of life. In other experiments, flies were started in

high and in low densities and then changed to the opposite condition after the sixteenth day of life. It was found that crowding has the most marked effect on mortality in early life. Flies which survived densely crowded conditions in early life were nevertheless weakened so that when they were transferred to an uncrowded environment they did not live as long as they would have, had they never been crowded" (p. 39-40).

TABLE 7

Life-duration of Drosophila at different population densities

(Data of Pearl, Miner and Parker, 1927.)

INITIAL DENSITY (Imagines per bottle)	MEAN DURATION OF LIFE (days)
2	27.31 $\pm$ 0.58
4	29.32 $\pm$ 0.60
6	34.45 $\pm$ 0.65
8	34.20 $\pm$ 0.61
10	36.22 $\pm$ 0.72
12	34.31 $\pm$ 0.61
15	37.92 $\pm$ 0.66
20	37.07 $\pm$ 0.55
25	37.47 $\pm$ 0.49
35	39.43 $\pm$ 0.67
45	37.46 $\pm$ 0.51
55	40.04 $\pm$ 0.53
65	35.25 $\pm$ 0.45
75	32.34 $\pm$ 0.46
85	30.10 $\pm$ 0.36
95	27.17 $\pm$ 0.36
105	24.20 $\pm$ 0.32
125	19.60 $\pm$ 0.28
150	16.17 $\pm$ 0.24
200	11.93 $\pm$ 0.20

This intermediate density optimum for longevity has also been reported independently by Bodenheimer (1938) working with his Palestine strain of *Drosophila* and using different techniques. His data are summarized in Table 8. Bodenheimer says, "Pearl's classical results are therewith fully confirmed: longevity shows a clear-cut density optimum, and is shorter

when population density is lower or higher" (p. 56).

There seems to be no reasonable doubt that both undercrowding and overcrowding shorten the life-span of *Drosophila*. In other words, a co-operative response is induced by optimal density. What the coactions, as well as possible action-reactions, are that have such an important influence on adult *Drosophila* is not known. Allee (1931, p. 245) has suggested,

"... the reduction in length of life at sub-optimal densities may be an expression of the inability of the small populations present to gain control of "wild" organisms other than the food yeasts present in the culture, while the supra-optimal density effects may be related at least in part to food shortage and to excess of excretion products... we have here one

TABLE 8

Life-duration of Palestine Drosophila at different population densities

(Data of Bodenheimer, 1938.)

Initial imago density (pairs)....	2	4	8	16	32	64
Mean life-duration (days)....	12.0	28.5	37.0	37.4	37.4	16.0

of the most suggestive of the phenomena yet presented."

This, of course, is partly conjecture. The analysis of the causal factors involved in the whole question is a problem worthy of warm welcome.

There is another aspect of *Drosophila* mortality that should be mentioned here for the sake of the record although there is little experimental information about it at present. This concerns pre-imaginal or metamorphic mortality as influenced by density. We have seen and will see further the importance of this in *Tribolium* populations. For *Drosophila* there is only the suggestion of Winsor (1937) who says,

"... the data on fecundity and fertility relative to density of population in *Drosophila* indicate a pre-

imaginal mortality varying markedly with density. This mortality may reach 90 to 99 per cent at high densities such as correspond to saturation levels of population. It seems highly probable that this mortality is a factor of major importance in the regulation of numbers" (p. 351).

This is another first-rate problem requiring the attention of the population student.

The suggestion that there is a relation between fly and yeast populations may illustrate in itself a significant co-operative coaction. Hammond (1939, p. 35) recognizes this point when he says, "A loose symbiosis exists between yeast and *Drosophila*, the yeast being spread by the flies which depend upon it to synthesize many non-protein compounds into proteins for themselves." There is a close corollary of this problem in that the flies may control to some extent the growth of mold as well as of yeast. If this is true it is another example of co-operation. Here then are two possible coactions awaiting quantitative analysis. Eigenbrodt (1925) has presented some data that are pertinent. This paper is summarized by Allee (1931, p. 148) as follows:

"The observations of Eigenbrodt that *Drosophila* grow larger in small culture vials when present in numbers of from 8 to 16 than at other population densities may be explained on the assumption that too few *Drosophila* larvae per culture fail to control the growth of harmful elements of the yeast or bacterial flora as well as optimal numbers do, while overcrowding overcontrols the growth of the food plant. This would result in a growth optimum occurring, as suggested, at a relatively low population density but distinctly above the minimum populations studied."

The two outstanding cases of co-operation for *Drosophila* have been presented: population optimum for longevity and fly-yeast (or mold) ratio. In the section on competition we shall discuss density of population in relation to egg production and show that the latter response is

adversely affected by crowding. However, before leaving this section a possible co-operation effect analogous to the initial optimal situation in *Tribolium* can be suggested. It must be stressed that this effect is not put forward as knowledge but merely as a possibility and stimulus for further research. In his 1932 paper, Pearl published a table (his Table 5) showing clearly that fecundity in *Drosophila* fell off with population density. There was one discrepancy in these data. The table shows the following oviposition rates for the quarter-pint bottle cultures in terms of "eggs per 1000 female hours' exposure":

Initial density (pairs per bottle)	Eggs
1.....	733.0
2.....	839.0
4.....	658.5
8.....	567.5

It is apparent at once that the two-pair population for *this case* has a much higher fecundity performance than the 1, 4, or 8 populations. This may be merely a chance deviation; however, it is enough like the original suggestion in Chapman's paper on *Tribolium* to warrant further analysis. Murroughs (1940) presents some preliminary data that suggest such an effect may be a real one for *Drosophila* populations but his results are not yet conclusive.

Disoperation

Tribolium. Earlier, we discussed the conditioned flour problem as an aspect of reaction. It was pointed out that conditioning is a modification imposed on the habitat by the population. It was also stressed that this modification is deleterious in its action. It causes population decline by adversely affecting reproduction and post-embryonic development. The position was adopted that it is difficult to

differentiate between conditioning as reaction and conditioning as disoperation. This differentiation can be accomplished on hypothetical grounds by assuming that, of the total conditioned flour produced by a particular culture, one increment depends on the summed influence of *individual* beetles on their habitat while the other increment depends on the summed influence of *inter-individual* beetle behavior (coaction) on the same habitat. Obviously, these two increments are not equal fractions of the whole necessarily. Although this is an entertaining theoretical distinction it is not too valuable in a pragmatic analysis of *Tribolium* population dynamics. However, there is one phase of conditioning that may be discussed more under the category of disoperation than reaction. This is the *rate* at which a culture manufactures conditioned flour. It can be shown for a constant time interval that conditioning varies in direct ratio to density. It is true that this rate phase is due to reaction but it is due more perhaps to disoperation since the disoperative coactions compound as population density increases. When flour is conditioned such effects as reduction of nutritive level and increased contamination occur. These are reactions. As *Tribolium* populations get more crowded, however, contacts between beetles and competition pressures increase. These are coactions. Obviously, not all these coactions are concerned with conditioning but some undoubtedly are.

A recent study (Park, 1938) can serve as an illustration of this rate effect. Experiments were designed to analyze the relation of habitat conditioning to the "efficiency" of *Tribolium* metamorphosis. Efficiency was measured by studying as groups the duration and mortality of the larval and pupal period. In setting up the experiments a series of populations,

ranging in density from one to 256 larvae per bottle, were established. All beetles were started in four grams of fresh (i.e. unconditioned) flour. Each bottle was examined at 48 hour intervals and deaths were recorded. The flour was not replaced at any time during the experiment. The results are quite clear-cut. Tables 9 and 10 show that, as larval crowding gets more severe, rate of larval development

TABLE 9

Larval and pupal mortality of Tribolium relative to different larval densities

(Data of Park, 1938.)

DENSITY (larvae per gram flour)	LARVAL MORTALITY (per cent)	PUPAL MORTALITY (per cent)
0.25	9.4	1.6
1.0	7.8	6.2
4.0	39.1	26.6
8.0	75.0	46.9
16.0	108.6	56.2

TABLE 10

Duration of the Tribolium larval period relative to different larval densities

(Data of Park, 1938)

DENSITY (larvae per gram flour)	MEAN LENGTH OF LARVAL PERIOD (days)	STANDARD DEVIATION (days)
0.25	38.3 $\pm$ 0.41	4.9 $\pm$ 0.28
1.0	38.7 $\pm$ 0.41	4.9 $\pm$ 0.28
4.0	52.0 $\pm$ 0.95	11.3 $\pm$ 0.67
8.0	92.1 $\pm$ 2.53	30.1 $\pm$ 1.78
16.0	141.4 $\pm$ 2.22	37.8 $\pm$ 1.58

strikingly decreases and larval and pupal mortality increase. The data may be interpreted in this fashion. In the experiments the flour becomes cumulatively more conditioned with age and crowding. The higher densities condition their habitat at a much faster rate than the lower densities as evidenced by performance during metamorphosis. This conditioned flour acts back on the developing population causing the results noted. It was

proved that the density effect was due to conditioning rather than to inter-beetle competition (coaction) for, when the flour was kept from getting conditioned by changing to fresh flour every 48 hours, the crowded larvae passed through their metamorphosis about as efficiently as the isolated larvae. A later investigation (Park, Miller and Lutherman, 1939) has shown that the same effects on larval and pupal mortality can be obtained if the flour is conditioned by imagoes instead of by larvae.

This study on metamorphosis suggests that the habitat is conditioned both by reaction and disoperation with every beetle thus participating in the primary and secondary cycles of cause and effect. The study was introduced under disoperation rather than reaction to suggest that disoperations may be more influential in controlling the rate of conditioning than reactions. It will be apparent to the critical reader, however, that this is essentially an arbitrary and perhaps unimportant position. In short, on the basis of knowledge to date it is impracticable to differentiate between reaction and disoperation when applied to the *Tribolium* conditioning problem. This is not necessarily a criticism of the ecological concepts themselves; it is an admission of our inability to distinguish them, with any cogency, in this instance.

An interesting case of disoperation can be constructed from a report of Chapman's (1926). This writer observed that if *Tribolium* imagoes were stimulated by rubbing they released a gas into the habitat "... which smells not unlike an aldehyde. It irritates the mucus membranes of the nose and turns flour and certain other materials pink, and in high concentrations, affects the eyes" (p. 295). It was shown that when larvae were

exposed to this gas about 10 per cent of them underwent abnormal development.

"The monsters produced by altering the larval transformation are usually winged larvae. . . . A series of forms has been produced in which one can follow the development of the wing pads from the smallest projections from the sides of the thorax to full-sized pupal wing pads. . . . The larvae which have responded in this way have been those which were in the last larval instar at the time they were exposed to gas. Consequently, the molt which produced the winged larvae was the one which would normally produce the pupae" (p. 296).

These abnormal larvae did not pass through their pupal period. Chapman showed that if the pupae were subjected to the gas they would emerge as teratologic imagoes. Similar cases, known as prothetely and metathetely and due to other causes, have been reported for *Tribolium confusum* by various writers (see Nagel, 1934; Oosthuizen and Shepard, 1936; Wigglesworth, 1939).

I have noted this gas many times in *Tribolium* cultures and have also seen abnormal larvae. In all such cases the imagoes were crowded intensely and their movement was increased markedly by the presence of their fellows. This is clear-cut disoperation since (1) the imagoes are stimulated by the behavior of their neighbors (coaction); (2) as a result of this coaction the gas is liberated; (3) the gas modifies the habitat—both flour and atmosphere; and (4) this modification has a deleterious influence on larval development. Obviously, this is not an important coaction in *Tribolium* cultures because of its infrequency. But it is an excellent illustration of disoperation in the Clements-Shelford sense and as such merits our interest.

Recently, Stanley (1938) has reported some data for *Tribolium* that are instructive examples of disoperation. His experiments are well summarized in his own words as follows:

"Experiments are described in which adults of *Tribolium confusum* Duv. are maintained at 27°C., and 75 per cent relative humidity in four different media: (a) ordinary whole wheat flour sifted through 76-mesh bolting cloth, (b) similar flour with from 30 to 135 *Tribolium* eggs per gram, (c) sifted whole wheat flour plus 3 per cent of finely ground wheat germ and (d) Flour plus germ plus eggs. It is shown that when large numbers of eggs are eaten, there is a serious decline in egg production unless wheat germ in excess is also present. This is believed to be due to a scarcity of certain accessory growth substances found in wheat germ but not to the same extent in eggs" (p. 300).

In this case the *Tribolium* add eggs to their habitat as they would any other metabolic by-product. This is a coaction response because oviposition depends on copulation contacts. The eggs are eaten indiscriminately along with flour. If eaten excessively, without supplementary wheat germ, the cannibalism results in disoperation by reducing the fecundity of female beetles. The possible stimulating effect of eggs plus flour plus germ if real should prove to be an illustration of co-operation. This is suggested by Stanley's statement (p. 300), "When ground wheat germ is present, the beetles seem to do somewhat better in the presence of eggs, possibly because of a better water supply, obtained from the eggs." This is an enticing suggestion awaiting further empirical analysis.

Drosophila. Unfortunately, I am unable to find any good illustration of disoperation for *Drosophila* populations. Obviously, this does not mean that this coaction system is not working within these cultures; it means either that I have overlooked a case already in print or else there is no such report as yet. The "intoxication" effect suggested by Bodenheimer was dealt with under reaction. Possibly it belongs here too but the data are so meagre that nothing more can be said at the moment.

Competition

As discussed earlier we shall view competition as a population pressure resulting from the demand made by many organisms on a limited supply of raw material. This demand does not lead necessarily to a specific end-effect in terms of total population success although it is deleterious usually from a short-time viewpoint.

Tribolium. An interesting case of competition occurring among *Tribolium* populations is cannibalism. This phenomenon was first noted by Chapman (1928) and has been analyzed further by Stanley (1932), Park (1932, 1933, 1934a), and Chapman and Baird (1934). We have discussed it under co-operation as a process working in conjunction with copulation frequency to bring about an initial optimal density effect. Here, we are interested in it as a competitive coaction. In a sense, cannibalism is a predator-prey relationship with larvae and imagoes the predators and eggs and pupae the prey. The possible competition coactions are as follows: (1) larvae with larvae; (2) larvae with imagoes; and (3) imagoes with imagoes. In all cases the prey is limited. However, the density of eggs and pupae, as well as the density of larvae and imagoes, controls the intensity of competition. When the predators are numerous and the prey sparse competition is severe; when the predators are few and the prey numerous competition is moderate.

It has been shown in the laboratory (Park, 1933) that (1) imagoes follow a random pattern of movement through their medium and may eat eggs as they come upon them, and (2) males, virgin females, and fecundated females eat eggs at a statistically equivalent rate. The latter point is supported by the data of Table 11. In Table 12 egg eating rates are given for male beetles maintained at

different population densities. These data corroborate the point made above that cannibalism varies directly with predator concentration.

What is the importance of cannibalism in terms of the total population? This question has been analyzed partially by Chapman (1928) who showed that under controlled habitat conditions *Tribolium* populations eventually reach an equi-

TABLE 11
Egg-eating rates of imago Tribolium
(Data of Park, 1933.)

PREDATOR	NUMBER TESTED	MEAN NUMBER EGGS EATEN PER BEETLE PER 11 DAYS
Males.....	40	7.1
Virgin females	40	7.3
Fecundated females...	40	6.5

TABLE 12
Egg-eating relative to imago density
(Data of Chapman and Baird, 1934.)

MALE DENSITY (imagos per gram)	PERCENTAGE REDUCTION OF A CONSTANT NUMBER OF EGGS OVER 7 DAYS
0.5	10.3
1.0	11.0
2.0	13.2
4.0	13.8
8.0	25.9
16.0	40.0

librium point in terms of beetles per gram of flour that is constant regardless of the initial density conditions. He explained this equilibrium somewhat as follows. In young, growing populations the imagoes and larvae are not numerous as they are in older cultures so that the eggs have a better chance of hatching into larval forms. As the population approaches its asymptote more eggs are being produced, since more females are present; but, also, more eggs are being eaten. The actual

equilibrium, according to Chapman, represents a condition where the relation between number of eggs laid and number consumed is fairly constant and is a situation, of course, in which the maximum *effective* reproduction occurs. In a later paper, Chapman and Whang (1934) analyzed further some of these relationships and showed that during early population growth the eggs, larvae, and pupae undergo fluctuations in numbers due, at least in part, to cannibalistic pressure. While I think the equilibrium mechanism pointed out by Chapman is highly over-simplified, nevertheless, it does furnish an excellent illustration of the rôle played by an important competition pressure in shaping population growth.

We can summarize this case of cannibalism as an example of competitive coaction as follows: (1) imago and larval *Tribolium* move at random through the flour; (2) eggs and pupae, as well as imagoes and larvae, are distributed randomly through the flour in varying but always *limited* numbers; (3) the former may eat the eggs, and to a lesser extent the pupae, as they encounter them; this is the behavioristic basis for the coaction; (4) the coaction or competition is the aggregate cannibalistic pressure as it occurs in the entire culture; (5) this competition varies with the numerical density of predator and prey and has definite end-effects on the population life-history; and (6) the competition is for food primarily and possibly for water secondarily.

The case of *Tribolium* cannibalism is an example of intra-specific competition. Competition can also be viewed from an inter-specific aspect. There are a number of excellent illustrations to be found in the literature dealing with micro-organisms;

for example, populations of *Paramecium* and *Didinium*, *Paramecium* and yeast, etc. These are well reviewed by Gause (1934) and fall somewhat outside the scope of a paper devoted to insects. Suffice it to say that most of these coactions are competitions for space and food.

A recent paper (Park, Gregg and Lutherman, 1941) reports studies dealing with inter-specific competition between three species of grain beetles: *Tribolium confusum*, *Gnathoceros cornutus* (both tenebrionids), and *Trogoderma versicolor* (adermestid). This investigation is not yet complete so that a full summary is impossible at the moment. However, certain relevant points can be made. The quantitative results are essentially clear; the coactions involved are not yet analyzed. In these experiments a medium was developed that (1) proved suitable for all three species, and (2) could be sifted for census taking. The total habitat was kept as optimal as possible by replacing the medium at each examination period; by using the same volume of flour in all populations, and by maintaining temperature, relative humidity, and light at certain constant points. At regular intervals counts of larval, pupal, and imaginal beetles were taken. The populations were set up as follows: Control A, consisting of one species only; Control B, consisting of two species introduced in initially equal densities; and Experiment C, consisting of various species' combinations with one form introduced at a numerical advantage over the other. These experiments have been under way for over 700 days with regular examinations at 30 day intervals. The following tentative conclusions can be advanced: (1) as single species populations *Tribolium*, *Gnathoceros*, and *Trogoderma* give evidence of some cyclic fluctuation or oscillation in numbers with age; (2) in mixed popula-

tions *Trogoderma* and *Gnathoceros* typically are driven out by *Tribolium*, irrespective of initial densities although under certain conditions *Gnathoceros* drives out *Tribolium*, and (3) in mixed populations *Trogoderma* and *Gnathoceros* are more closely matched although *Gnathoceros* appears to be favored somewhat. Obviously there is fodder here for a long discussion. Our point may be made by focusing attention on conclusion 2 above. Here is a case where one species eventually drives out another. In this instance habitat modifications (action, disoperation, and reaction) are minimized by maintaining experimentally the habitat as optimal as it is possible to do so. Even so, one population controls another and eventually supplants it. To a large measure this control must result from coactions between both competing species. These species are exploiting some common, but limited, material or source of energy. The naming and delineation of the particular coactions involved in this case must await further experimentation. We do have here, however, an example of inter-specific population pressure where the control is apparently due to competition.

Drosophila. As an example of competition in fruit-fly populations the effect of population density on fecundity may be discussed. In 1922, Pearl and Parker set up initial populations of flies at concentrations ranging from one pair per half-pint bottle to 50 pairs per half-pint bottle and counted the number of progeny produced by the different densities. They were able to show that as the population density increased the number of offspring per bottle decreased. In other words, productivity stood in inverse ratio to population density. The authors made no attempt to explain this descriptive result at the time, simply pointing out

that the phenomenon was one characteristic of many types of populations.

In a later paper, Pearl (1932) designed experiments to answer these questions: (1) what physiological process or processes which would explain the type of result just summarized is influenced by density, and (2) what factor or factors, dependent upon density, influence this process? In considering the first point it was reasoned that in short-lived populations where mortality was not important the rate of reproduction must be the factor varying between the different densities. That is to say, the flies would have to reproduce faster at low densities than at high to explain the observed results. This differential in reproduction could be due to an alteration of fecundity, of fertility, or both. Experiments were started in which the initial densities varied in geometric series from one to 128 pairs of *Drosophila* per bottle. The eggs were collected at regular intervals from each container and counted. It was shown that the fecundity was greatly influenced by the number of imago flies in the bottle, since the oviposition, expressed as a rate per female per day, fell off rapidly as the density increased. No important relations between fertility and density were reported; this remains an excellent problem for experimental attack.

From this particular analysis two facts emerge: (1) the description of a specific relationship between population density and population growth, and (2) the demonstration that this relationship is due, in part at least, to a differential alteration of fecundity performance. An analysis of the factors actually influencing the fecundity logically follows as the next step. To answer this question Pearl set up experiments in which the air volume in the bottles above the medium

was varied but the area of agar surface was kept constant. The results are summarized in Table 13. It was found that, while the extent of the air space above the culture medium had no significant effect on oviposition, the extent of crowding of the flies on the agar surface was highly important in altering their fecundity. To put differently, the real density effect occurs when the flies are crowded together on this surface.

TABLE 13

Oviposition of Drosophila on a constant agar surface area under varying conditions of density and air volume

(Data of Pearl, 1932.)

INITIAL DENSITY P(pairs per bottle)	EGGS PER 1000 FEMALE HOURS' EXPOSURE	
	Half-pint bottles	Quarter-pint bottles
1	869.8	733.0
2	606.2	839.7
4	529.0	658.5
8	557.1	567.5
16	340.6	338.0
32	176.6	186.7
64	104.4	129.4
128	108.5	120.8
Mean	178.5	201.7

Bodenheimer (1938) reports experiments that substantiate the conclusion just advanced; namely, that agar area is the important factor in shaping *Drosophila* productivity. He set up three series of experiments in which the relation of (a) volume of agar and (b) volume of air space to total population size was assayed. In all series the exposed agar surface was the same. The data are tabulated in Table 14 from which it is apparent that all the populations reach a similar asymptote irrespective of the two experimental variables.

Thus the possible action, reaction, and

coaction processes which control population fecundity have their major origin in agar surface relationships. As in the *Tribolium*, *Gnathoceros*, *Trogoderma* case earlier discussed, the rôle of the primary cycle and disoperation is somewhat minimized in Pearl's experiments since he supplied the flies with fresh agar daily. This suggests that coaction is involved. This coaction must be competition and not co-operation because the effect of increasing density is injurious in terms of culture growth. Pearl made elaborate observations on the behavior of imago *Drosophila* under conditions of minimal

other primarily for food and oviposition niches. This competition results in a lowered fecundity. Since the coactions compound with density, fecundity drops off rapidly as the flies get more crowded. Finally, this reaches a place, above 100 flies per bottle, where egg production is not affected further to any appreciable extent.

Inter-specific competition in fly populations

A recent paper by Vladimerova and Smirnov (1938) reports some interesting data on competition, and to a lesser extent co-operation, in populations of *Musca domestica* and *Phormia groenlandica*. In this study both single species and mixed species larval cultures were set up. The data are well summarized by Trager (1940) in *Biological Abstracts* (May) in the following words:

"Larvae of both species of flies were placed, two hours or less after hatching, in counted numbers on weighed pieces of beef liver. By increasing the number of larvae, the amount of food available per larva was decreased. The cultures were kept at 25°C., and were allowed to pupate in sand. The number and weight of pupae obtained were determined. In homogeneous populations of each species the mean pupal weight decreased with increasing number of larvae per gram of food, rapidly at first and then more slowly to a minimal value. The total mass of pupae produced increased at first, almost in direct proportion to increase in the number of larvae until it reached a maximum and fell off with further increase in numbers. At the same time, the percentage of survival also decreased. In mixed populations, the relation between mean pupal weight and population density remained the same. However, for *Musca*, the total mass of pupae continued to increase farther with increasing original population and reached a higher maximum than in pure populations, while the reverse was true for *Phormia*. Larvae of the latter are apparently more sensitive to crowding and die off sooner."

and maximal crowding. He reached the conclusions that (1) the flies will not oviposit if they are in contact with, or disturbed by, other flies; (2) crowded flies stimulate each other so excessively that energy is dissipated that might otherwise be used in reproduction; and (3) individual imagoes do not obtain their full share of food (from the agar surface) under these crowded conditions due to the disturbance of their feeding behavior brought about by their neighbors. The latter point holds true even though there is more than enough food present for the total imaginal population. Plainly, these are competitive coactions. As cultures get more crowded flies compete with each

TABLE 14
Further data on volume and area relationships in
Drosophila fecundity
(Data of Bodenheimer, 1938.)

EXPERIMENTAL VARIABLES	SERIES		
	1	2	3
Agar surface $\frac{1}{2}$ (diameter cm.) . . .	5.5	5.5	5.5
Agar volume (c.c.) . . .	26.4	26.4	52.8
Air volume (c.c.) . . .	149.6	74.8	74.8
Asymptotic population (maximum no. flies) .	206.	205.	205.

From our viewpoint this study is significant in three ways: (1) it provides a new illustration of inter-specific population pressure using new laboratory animals; (2) it implements further the notion that, as population density in-

creases, certain coactions result in intensified competition for food followed by noticeable retardation of growth; and (3) it suggests a new instance of co-operation linked intimately with competition within a single microcosm. The last point emerges from the investigation since it is shown that, in the mixed populations, *Musca* produce a greater total mass of pupae than they do in single species cultures. In short, there is something stimulating for the housefly (*Musca*) that grows out of its association with *Phormia*. On the other hand, the latter species has its pupal production retarded by association with *Musca*. This is probably a case of competition primarily (e.g. for food) although more evidence is needed before a definite conclusion can be reached. There are some pregnant problems awaiting attack here. Along these lines a paper by Omori (1939) on the "cohabitation" and cross-mating of two species of *Cimex* (*C. lectularius* and *C. hemipterus*) should be examined also.

DISCUSSION

We have now covered in some detail certain of the major ecological concepts developed by Clements and Shelford and have illustrated these concepts with examples taken from the literature dealing with *Tribolium* and *Drosophila*. We may spend with profit a short time in stock-taking. Let us examine for a moment the growth of a *Tribolium* population and then attempt to relate briefly that growth to some of the ideas developed in this paper. Earlier it was mentioned that Bodenheimer divides the growth of *Drosophila* cultures into four consecutive periods: (1) Period of initial growth, (2) of rapid growth, (3) of oscillations, and (4) of contraction. Although we lack much real information about the factors causing these periods, we can apply them to flour-beetle popula-

tions as *descriptive* stages of a continuous time-cycle. As with *Drosophila*, the periods of initial and rapid growth in *Tribolium* are well summarized by the logistic curve. Gause (1931) has fitted the data of Chapman (1928) to a logistic with not unreasonable deviation. Assuming that this curve is a good smoothed description of the way a *Tribolium* population grows, certain deductions about the character of that growth may be made. Such rationalizations are stressed by Gause (1934) and, from a more empirical viewpoint, by Bodenheimer (1937). The latter has applied certain arithmetical computations to the data of Chapman that are designed to aid in understanding the gross intra-population dynamics. The experimentalist will recognize immediately that these calculations merely serve to emphasize aggregate or statistical pressures; usually they do not clarify the finer actual mechanisms and, at times, really obscure them by lumping a number of items together. An example of this is in order. Chapman (1931) has shown that during *Tribolium* culture growth there is,

"First a steady increase in number of eggs present. After some days the first laid eggs begin to hatch and there follows an increase in the number of larvae, and coincidentally with the increase in larvae there is a decrease in the number of eggs present. The next stage is that in which the larvae commence to pupate and the pupa population increases simultaneously with a decrease in the population of larvae. The egg production again rises, and now pupae begin to hatch producing an increase in the adult population which eventually reaches a steady state, while larval and egg populations continue to fluctuate about a stable mean. These fluctuations are best explained by treating the larvae and adults as predators of the eggs, which are themselves being produced by the adults. Thus the first decrease in eggs takes place when the larvae hatch, and it continues, owing to the predatory action of the larvae, until the larval population is reduced by pupation, which, of course, allows the egg population to rise." (Quotation from Ford, 1937; p. 11.)

Here, certain mechanisms based on life-history data are camouflaged by statistical grouping. Thus, for this case, points of a smoothed growth curve based on total population census would obliterate these oscillations exhibited by the population components. But the statistical calculations are useful if (a) accepted with certain critical reservations plus knowledge of the biology of the species in question and (b) fitted to basically sound data.

Bodenheimer's calculations, summarized in Table 15, are based on cultures growing

in terms of the periods of initial and rapid growth certain general conclusions are evident. For the initial period the imago population is small and, after an early spurt, the rate of growth lowers to essentially a constant point. This early spurt may reflect co-operative coactions such as were discussed under the initial population optimum. During the early growth period the environmental resistance (also from Chapman; the environmental check on increase) and the intensity of the struggle for existence are low. In part,

TABLE 15
Population trend and analysis of 100 days' growth of a Tribolium culture
(Computations of Bodenheimer, 1937.)

AGE (days)	A Total population	B Adult population	C Potential increase of population	D Actual no. of eggs per day	E Realization of the poten- tial increase	F Environmental resistance	G Rate of growth	H Intensity of struggle for existence
0	16	16	—	—	—	0.0	—	—
10	568	15	858	802	934.	0.066	35.5	23.2
20	563	14	751	237	315.7	0.685	1.0	750.
30	596	92	2468	168	0.068	0.932	1.1	2243.
40	760	35	9389	127	0.013	0.987	1.3	7221.
50	791	362	7769	344	0.044	0.956	1.1	7062.
60	844	373	20065	1040	0.050	0.950	1.1	17331.
70	1056	362	19421	1559	0.080	0.920	1.3	14938.
80	1138	364	19529	1722	0.088	0.912	1.1	17753.
90	1286	361	19421	2068	0.106	0.894	1.1	17655.
100	1299	357	19207	2106	0.109	0.891	1.0	19206.

at 32°C., and 75 per cent relative humidity in whole-wheat, sifted flour. Many of the entries in the table are obvious. Column C shows the total possible population fecundity; in Chapman's words the

"biotic potential." Column $E = \frac{D}{C}$ and

Column $F = 1 - E$. Column $G = \frac{\text{total population}}{\text{total population of previous census}}$ and

Column $H = \frac{C}{G}$. If we examine the table

this is an expression of the fact that cannibalism is not too severe. This is the period when the potential reproductive performance is nearest actual realization. As the population moves into the period of rapid growth, the imagoes soon reach their equilibrium and the increase of immature stages begins to slow down. The culture approaches its asymptote and the rate of growth stabilizes to a point where it merely maintains the population at essentially an even level. The environmental resistance and the intensity of the

struggle for existence have grown to a maximum. There is but a small increment of realization of the potential increase.

Not too much is known about the period of oscillations for *Tribolium* cultures. The general conception of such oscillations was developed by Volterra (1926) who phrased the so-called "laws" of population fluctuations: "Law of the periodic cycle"; "Law of the conservation of the averages"; and "Law of the disturbance of the averages." Certainly, nothing of this sort has been rigorously fitted to *Tribolium* populations. However, there is some experimental evidence to the effect that if excessive conditioning is kept from entering into the picture flour-beetle cultures do fluctuate about some equilibrium point. Chapman was not clear on this point in his 1928 paper. In a later paper (1933) he suggested that mass infection of cultures with a Sporozoan (*Adelina*, see Park, 1934a) caused oscillations. Ford (1937) says,

"*Adelina* is parasitic in *Tribolium* larvae, causing their death during the instar immediately preceding pupation. Thus in parasitized cultures no adults are produced, and the population gradually declines owing to the natural death of adults and consequent failure to maintain the egg production. During this decline the populations of eggs and larvae fall into fluctuating rhythms which alternate with one another. Eggs are continually being produced thus tending to an accumulation of eggs. Meanwhile larvae hatch from the eggs, on the remainder of which they feed. There is here the mechanism of fluctuations between predator and prey . . . and such fluctuations were found to occur in both accidentally and experimentally parasitized cultures. The parasite, by removing the pupal and adult stages from the population, has the effect of once more starting the larva-egg fluctuation with which a *Tribolium* population commences" (pp. 11-12).

In my laboratory I have recently observed also that *Tribolium* cultures oscillate with time about an average. The magnitude and the interval of the oscillations is

somewhat variable but, nevertheless, they appear as true population realities. This work is now in process of analysis.

The conditioning experiments offer information pertinent for the period of contraction. For this final period some of the channels through which contraction operates—lowered fecundity, aberration of metamorphosis, etc.—are known. As far as results to date go, the conditioned flour studies suggest that, if the flour is not frequently renewed, *Tribolium* through conditioning start limiting their future population as far back as the period of initial growth. This conclusion is based on data (Park, 1936a, 1938, 1938a, Park and Woolcott, 1937, Park, Miller and Lutherman, 1939) which show that even slight amounts of conditioned flour have deleterious effects on certain of the beetles' responses. Suffice it to say that a definite period of contraction is known for *Tribolium* and some of the essential causal factors have been studied.

Pearl (1927) pointed out that the population student, whether field, or laboratory, or human, is concerned with two biological processes ultimately; natality or the forces of reproduction, and mortality or the forces of death. Furthermore, the student is interested in the factors, not in regard to individual organisms, but as statistical end-expressions of the activity of total aggregations. Thus the population is rooted by its basic biological variables to responses that are meaningless when viewed in other terms. In short, through its integration the population emerges as a new unit; a unit that possesses its own set of activities, its own particular environment, and its own heredity. (For an elaboration of this point see Emerson, 1939 and Park, 1939.)

In a number of the studies reviewed thus far we have seen how the population size at any moment of time depends on the

balance between total reproductive potentialities and the check or resistance exerted by the environment on these capacities. This check or "environmental resistance" may act either on birth-rate or on death-rate. In a stimulating paper Smith (1935) proposed that environmental resistance be split into two major components; "density-dependent" and "density-independent" factors, thus following a suggestion proposed by Howard and Fiske (1911). This is a recognition of the fact, already abundantly attested in this paper, that density thresholds are created by a population as it matures and these thresholds control, in part, the population's life-history. Factors that operate in this way are density-dependent and include such examples as predator and parasite relationships, diseases, intra-specific population pressure, spatial restrictions, food limitations (in part), and so on. These factors vary in their effect on a population as that population varies its density. To put it differently, environmental resistance is modified, in one direction or another, by crowding. In the category of density-independent factors belong largely such elements as climate (see Uvarov, 1931). These factors contribute an increment to the total population environmental resistance which does not vary with density. Let us take a stylistic example. Imagine a population, 100 X, that has a total environmental resistance of 50. Of this resistance at a given instant of time 30 is density-dependent and 20 is density-independent. If 100 X changes by growth to 200 X the density-independent environmental resistance remains 20 but the density dependent resistance changes, say, to 72. This change is not predictable. It must be assayed.

There are certain suggestions that can be made about the Clements-Shelford system as applied to *Tribolium* populations.

During the population's life-history the primary cycle is in continuous operation. There are always habitat actions on the beetles and beetle reactions on the habitat. Also, there is always aggregation and, by that token, always coaction in one or all of its aspects. These mechanisms, however, change in character, in mode of operation and in end-effect as the population matures in time and space. Thus the actions-reactions of the initial growth period are not necessarily the same as those in the period of rapid growth or the period of contraction. For example, during the latter period the action-reaction aspects of conditioning are of great significance as we have shown, while in the initial period they are not so important. Contrariwise, those reactions impinged by young populations on the flour that establish burrows and tunnels and other physical modifications are essential during the initial period but unimportant in the contraction period. However, both are population products and both are primary cycles. To that extent they play equivalent rôles in population control. As the population matures coactions shift in character and end-effect even more than do actions and reactions. Coactions are, of course, products of density and much more intimately linked with density-dependent factors than the action-reaction cycle. The latter, while it may be density-dependent in part, is frequently density-independent; that is to say, certain actions and reaction take place irrespective of crowding. This is not true for coaction. Environmental resistance is continually changing during a population's history and this change is caused largely by the dependence of coaction on density. The intensity of the struggle for existence is a case in point. It has been shown for cultures of microorganisms, *Drosophila*, *Tribolium*, and the honeybee

that this intensity, which is primarily an indicator of competition (although we may have co-operative and disoperative components), increases during the first two growth phases; fluctuates in causal relationship during the period of oscillation, and increases enough during the contraction period to initiate and continue the population's decline.

The reader will recognize two points: (1) that these controlling factors of the population are not mere dialectics; we have implemented many of them empirically and in considerable detail in this paper and future population research should permit greater implementation, and (2) that, with the important exception of migration, the basic forces operating in laboratory populations are a simplified counterpart of those operating in field communities. This last point is another way of saying that those concepts of Clements and Shelford discussed in this paper are comprehensive. They can be fitted to a diverse group of field communities as well as to experimental populations. Two questions suggest themselves to the critically minded biologist: (a) is there any advantage in this comprehensiveness, and (b) is it an artifact or an ecologic reality? I think the advantage lies in that the system gives the ecologist a working framework into which he can apportion diverse facts and thereby evaluate existing data, and, just as importantly, it enables him to recognize where the gaps in ecological knowledge lie and take steps to improve the situation. The concepts dealt with here are neither erudite nor abstruse. They are merely obvious ideas that aid in interpreting the environmental relations of organisms and their usefulness lies in this very point. As soon as ecology progresses further the concepts can be refined, or, if necessary, readily discarded.

But in all events it is the *progress* in which we are interested!

Early in this paper it was suggested that there are operational similarities between the field and laboratory population. This point stimulates the experimental work since the latter has for its first biological aim the ultimate interpretation of natural, ecological phenomena. To me, the agreement between Clements' and Shelford's system and the *Tribolium* and *Drosophila* studies supports this contention. It would be unfair, however, not to point out in passing that there are some *differences* between field and laboratory populations. Two such differences are especially obvious: (1) laboratory populations are overly simplified, and (2) laboratory studies have not analyzed to any extent migration and dispersal phenomena which are of great significance in natural communities. The first difference is really a common but pointless argument against the validity of the experimental work. I fail to see any real distinction between the ecologist, analyzing experimentally a population process in order to gain more insight into group integration, and a physiologist, analyzing experimentally the contractility of an excised muscle in a foreign solution in order to learn more about the muscular co-ordination of the entire organism. The general failure of the population student to examine migration in his experimental system is an argument of greater weight. Until this factor is subjected to successful experimental analysis the laboratory population student cannot consider that he has concerned himself with all the basic similarities that exist between field and laboratory groups. Contrariwise, there is much that the field student can learn by applying the experi-

mental techniques developed in the laboratory over to field problems.

The final point to be discussed is the status of the philosophical position taken by Clements and Shelford. It will be remembered that they suggested that the community is a social organism and they held that this aided them in making their interpretations. After working through this material on the experimental population as an illustration of a general ecological system I find myself concluding (1) that the population or a community is such a social or supra-organism, and (2) that this interpretation adds something to an understanding of the population. To me the supra-organismic concept is more meaningful when applied, say, to social insect populations than to *Tribolium* or *Drosophila*. However, it does aid in focusing attention on the unity of the population by stressing the analogies or convergences between an individual organism and an organism group and by showing that this unity is in part a product of natural selection. Natural selection thus emerges as a common denominator regardless of the level of biological organization.

It may be appropriate to discuss further what is implied when the population is referred to as a unit. By unit I mean that the group emerges with certain tangible properties, both statistical and biological, not possessed by its components. We may express our meaning of unit in symbolic terms. Assume a population composed of a series of individual organisms symbolized as X. Each X has a complete set of biological attributes designated as Y. If the population does not behave as an integrated whole, a group 1000 X will have properties 1000 Y. However, there are abundant data to show that the Y component of 1000 X is not the simple sum 1000 Y but, say, 750 Y or 1237 Y. It is this

deviation that emerges as a population property, a result of aggregation and subsequent organization of the aggregants. Obviously, there is nothing in the slightest new in this position. Morgan (1933, see also a review by Wright, 1935) and Wheeler (1928) and much earlier Spencer (1860) among others have made these suggestions. The essential point is that the ecologist or population student must focus his attention on the deviation since this is a true population characteristic. This is a helpful conclusion but I think it must be reached first by empirical analyses of the populations themselves with the supra-organismic analogy emerging secondarily. To my mind, the real value of the latter analogy is philosophical rather than technical. It aids in synthesizing a perspective in which biological groupings of different levels of complexity can be placed one with reference to the other.

SUMMARY

The primary concern of this paper is to show that laboratory populations and natural field communities have many biological and statistical similarities. This viewpoint is developed by (1) discussing critically certain major concepts of the ecological system of Clements and Shelford; (2) illustrating these concepts in some detail with experimental investigations taken from the literature dealing with *Tribolium confusum* and *Drosophila melanogaster* populations; and (3) synthesis of the material developed under points one and two.

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LITERATURE CITED

- ALLEE, W. C. 1931. Animal Aggregations. A Study in General Sociology. *Chicago* (University of Chicago Press). Pp. 421.
- 1934. Recent studies in mass physiology. *Biol. Rev.* 9 (1), pp. 1-48.
- 1938. The Social Life of Animals. *New York* (W. W. Norton and Co.). Pp. 293.
- 1940. Concerning the origin of sociality in animals. *Scientia*, April, pp. 154-160.
- ALLEE, W. C., and THOMAS PARK. 1939. Concerning ecological principles. *Science*, 89 (2304), pp. 166-169. Feb. 24.
- ALPATOV, W. W. 1932. Egg production in *Drosophila melanogaster* and some factors which influence it. *Jour. Exp. Zool.*, 63: pp. 85-111.
- ALPATOV, W. W., and RAYMOND PEARL. 1929. Experimental studies on the duration of life. XII. Influence of temperature during the larval period and adult life on duration of life of the imago of *Drosophila melanogaster*. *Amer. Nat.*, 63: pp. 38-67.
- BODENHEIMER, F. S. 1938. Problems of Animal Ecology. *London* (Oxford Univ. Press). Pp. 183.
- CHAPMAN, ROYAL N. 1926. Inhibiting the process of metamorphosis in the confused flour beetle. *Jour. Exp. Zool.*, 45: pp. 293-299.
- 1928. Quantitative analysis of environmental factors. *Ecology*, 9: pp. 111-122.
- 1931. Animal Ecology with Special Reference to Insects. *New York* (McGraw-Hill Co.). Pp. 464.
- 1933. The cause of fluctuations of populations of insects. *Proc. Hawaii Ent. Soc.*, 8: pp. 279-297.
- CHAPMAN, ROYAL N., and LILLIAN BAIRD. 1934. The biotic constants of *Tribolium confusum* Duval. *Jour. Exp. Zool.*, 68: pp. 293-304.
- CHAPMAN, ROYAL N., and W. Y. WHANG. 1934. An experimental analysis of the cause of population fluctuations. *Science*, 80: pp. 297-298. Sept. 28.
- CHILD, C. M. 1924. Physiological Foundations of Behavior. *New York* (Holt and Co.). Pp. 330.
- CLEMENTS, F. E., and V. E. SHELFORD. 1939. Bio-Ecology. *New York* (John Wiley and Sons). Pp. 425.
- DICK, JOHN. 1937. Qviposition in certain coleoptera. *Ann. Applied Biol.*, 24: pp. 762-796.
- DORZANNEY, TH. 1935. Fecundity in *Drosophila pseudoobscura* at different temperatures. *Jour. Exp. Zool.*, 71: pp. 449-464.
- 1937. Genetics and the Origin of Species. *New York* (Columbia Univ. Press). Pp. 364.
- EIGENBRODT, H. J. 1925. The somatic effects of certain environmental conditions on a homozygous race of *Drosophila*. Ph.D. thesis in Univ. Ill. Library. Pp. 126.
- ELTON, CHARLES. 1940. American ecology. Being a review of Bio-Ecology by F. E. Clements and V. E. Shelford. *Jour. Anim. Ecol.*, 9: (1); pp. 148-149.
- EMERSON, A. E. 1939. Social coordination and the superorganism. *Amer. Mid. Nat.*, 21: (1); pp. 182-210.
- 1939a. Populations of social insects. *Ecol. Monog.*, 9: pp. 287-300.
- FISHER, R. A. 1930. The Genetical Theory of Natural Selection. *Oxford* (Clarendon Press). Pp. 272.
- FORBES, S. A. 1887. The lake as a microcosm. *Ill. Nat. Hist. Surv. Bull.*, 15: pp. 537-550.
- FORD, JOHN. 1937. Research on populations of *Tribolium confusum* and its bearing on ecological theory: a summary. *Jour. Anim. Ecol.*, 6: (1); pp. 1-14.
- GAUSE, G. F. 1931. The influence of ecological factors on the size of population. *Amer. Nat.*, 65: pp. 70-76. Jan.-Feb.
- 1934. The Struggle for Existence. *Baltimore* (Williams and Wilkins). Pp. 160.
- GERARD, RALPH W. 1940. Organism, society and science. (In three parts.) *Scientific Monthly*, Part I: April, pp. 340-351; Part II: May, pp. 403-413; Part III: June, pp. 530-536.
- GLEASON, H. A. 1939. The individualistic concept of the plant association. *Amer. Mid. Nat.*, 21: (1); pp. 92-111.
- GOOD, N. E. 1936. The flour beetles of the genus *Tribolium*. *U.S.D.A. Technical Bulletin* No. 498. Pp. 57.
- HALDANE, J. B. S. 1932. The causes of evolution. *London* (Longmans, Green and Co.). Pp. 235.
- HAMMOND, E. CUTLER. 1938. Biological effects of population density in lower organisms. Part I. *QUART. REV. BIOL.*, 13: (4); pp. 421-438.
- 1939. Biological effects of population density in lower organisms. Part II. *QUART. REV. BIOL.*, 14: (1); pp. 35-59.
- HARNLY, M. H. 1930. A critical temperature for lengthening of the vestigial wings of *Drosophila*

- melanogaster* with sexually dimorphic effects. *Jour. Exp. Zool.*, 56: pp. 363-368.
- HARRIS, F. H. 1939. Some temperature coefficients for insect oviposition. *Ann. Ent. Soc. Amer.*, 32: (4); pp. 758-776.
- HASKELL, E. F. 1940. Mathematical systematization of "environment," "organism" and "habitat." *Ecology*, 21: (1); pp. 1-17.
- HJORT, JOHAN. 1938. The Human Value of Biology. Cambridge, Mass. (Harvard University Press). Pp. 241.
- HOLDAWAY, F. G. 1932. An experimental study of the growth of populations of the "flour beetle," *Tribolium confusum* Duval, as affected by atmospheric moisture. *Ecol. Monogr.*, 2: pp. 261-304.
- HOWARD, L. O., and W. F. FISKE. 1911. Importation into the United States of the parasites of the gipsy and brown-tailed moths. *U.S.D.A. Bur. Entom. Bull.*, 91; pp. 1-312.
- HUTCHINSON, G. E. 1940. Bio-ecology. Being a review of Bio-ecology by F. E. Clements and V. E. Shelford. *Ecology*, 21: (2); pp. 267-268.
- LOBB, J., and J. H. NORTHROP. 1917. On the influence of food and temperature upon the duration of life. *Jour. Biol. Chem.*, 32: pp. 103-121.
- LOTKA, A. J. 1934. Théorie analytique des Associations biologiques. *Actualités Scientifiques et Industrielles*, No. 187. Pp. 45.
- MACLAGAN, D. S. 1932. The effect of population density upon rate of reproduction with special reference to insects. *Proc. Roy. Soc., B*: 111: pp. 437-454.
- and E. DUNN. 1936. The experimental analysis of the growth of an insect population. *Proc. Roy. Soc. Edmb.*, 55: pp. 126-139.
- MACLULICH, D. A. 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). *Biol. Ser. 43, Univ. Toronto*.
- MICHAL, K. 1931. Die Beziehung der Populationsdichte zum Lebensoptimum und Einfluss des Lebensoptimum auf das Zahlenverhältnis der Geschlechter bei Mehlwurm und Stubenfliege. *Biol. Generalis*, 7: pp. 631-646.
- MÖBIUS, K. 1877. Die Auster und die Austernwirtschaft. Berlin. Translated into English: 1883; *Proc. U. S. Fish Comm.*, 8: pp. 721-729.
- MORGAN, LLOYD. 1926. Emergent Evolution. New York (Henry Holt and Co.) Pp. 313.
- MORGAN, T. H., C. B. BRIDGES, and A. H. STURTEVANT. 1925. The genetics of *Drosophila*. *Bibliographia Genetica*, 2: Pp. 262.
- MURKOVICH, T. R. 1940. Effects of sex-ratio and population density upon fecundity in *Drosophila melanogaster*. Divisional Master's Essay; Univ. Chicago.
- NAOEL, R. H. 1934. Metathetely in larvae of the confused flour beetle (*Tribolium confusum* Duval). *Ann. Ent. Soc. Amer.*, 27: (3); pp. 425-428.
- , and H. H. SHEPARD. 1934. The lethal effect of low temperatures on the various stages of the confused flour beetle. *Jour. Agr. Res.*, 48: (11); pp. 1009-1016.
- NICHOLSON, A. J. 1933. The balance of animal populations. *Jour. Anim. Ecol.*, 2: pp. 132-178.
- , and V. A. BAILEY. 1935. The balance of animal populations. Pt. I. *Proc. Zool. Soc. London*, pp. 551-598.
- OMORI, N. 1939. Experimental studies on the cohabitation and crossing of two species of bed-bug, *Cimex lectularius* and *C. hemipterus* F. (Preliminary report). *Verb. 7 Int. Kongr. Ent. Berlin 1938*; 2: pp. 895-915.
- OOSTHUIZEN, M. J. 1935. The effect of high temperature on the confused flour beetle. *Univ. Minn. Agr. Exp. Sta. Tech. Bull.*, 107. Pp. 44.
- OOSTHUIZEN, J. J., and H. H. SHEPARD. 1936. Prothetely in larvae of the confused flour beetle (*Tribolium confusum* Jacq.-Duv.). *Ann. Ent. Soc. Amer.*, 29: (2); pp. 268-272.
- PARK, THOMAS. 1932. Studies in population physiology. I. The relation of numbers to initial population growth in the flour beetle *Tribolium confusum* Duval. *Ecology*, 13: (2); pp. 172-181.
- 1933. Studies in population physiology. II. Factors regulating initial growth of *Tribolium confusum* populations. *Jour. Exp. Zool.*, 65: (1); pp. 17-42.
- 1934. Studies in population physiology. III. The effect of conditioned flour upon the productivity and population decline of *Tribolium confusum*. *Ibid.*, 68: (2); pp. 167-182.
- 1934a. Observations on the general biology of the flour beetle, *Tribolium confusum*. *QUART. REV. BIOL.*, 9: (1); pp. 36-54.
- 1935. Studies in population physiology. IV. Some physiological effects of conditioned flour upon *Tribolium confusum* Duval and its populations. *Physiol. Zool.*, 8: (1); pp. 91-115.
- 1935a. Sterilization of *Tribolium* by high temperature. *Science*, 82: (2125); pp. 281-292. Sept. 20.
- 1936. Studies in population physiology. V. The oxygen consumption of the flour beetle, *Tribolium confusum* Duval. *Jour. Cell. and Comp. Physiol.*, 7: (3); pp. 313-323.
- 1936a. Studies in population physiology. VI. The effect of differentially conditioned flour upon the fecundity and fertility of *Tribolium confusum* Duval. *Jour. Exp. Zool.*, 73: (3); pp. 393-404.

- 1937. Experimental studies of insect populations. *Amer. Nat.*, 71: pp. 21-33. Jan.-Feb.
- 1937a. The culture of *Tribolium confusum* Duval. Reprinted from Culture Methods for Invertebrate Animals (edited by J. G. Needham). *Ithaca* (Comstock Publishing Co.). Pp. 463-466.
- 1938. Studies in population physiology. VIII. The effect of larval population density on the post-embryonic development of the flour beetle, *Tribolium confusum* Duval. *Jour. Exp. Zool.*, 79: (1); pp. 51-70.
- 1938a. A note on the size and composition of old *Tribolium confusum* populations. *Amer. Nat.*, 72: pp. 24-33. Jan.-Feb.
- 1939. Analytical population studies in relation to general ecology. *Amer. Mid. Nat.*, 21: (1); pp. 235-255.
- 1939a. Ecology looks homeward. Being a review of Plant and Animal Communities (Th. Just, Editor). *QUART. REV. BIOL.*, 14: (3); pp. 332-336.
- 1939b. Abstract. Interspecific competition in experimental laboratory populations. *Ann. Rec.*, 75: (4); Supplement, p. 159.
- , and WILLIAM BURROWS. 1939. Abstract. Preliminary nutritional studies on the reproduction of *Tribolium confusum* in a synthetic medium. *Ibid.*, 75: (4); Supplement p. 140.
- , ELLA VIRGINIA GREGG, and CATHARINE Z. LUTHERMAN. 1941. Studies in population physiology. X. Inter-specific competition in populations of granary beetles. *Physiol. Zool.*, 14: (4); pp. 395-430.
- , ELLA VIRGINIA MILLER, and CATHARINE Z. LUTHERMAN. 1939. Studies in population physiology. IX. The effect of imago population density on the duration of the larval and pupal stages of *Tribolium confusum* Duval. *Ecology*, 20: (3); pp. 365-373.
- , and NANCY WOOLLCOTT. 1937. Studies in population physiology. VII. The relation of environmental conditioning to the decline of *Tribolium confusum* populations. *Physiol. Zool.*, 10: (2); pp. 197-211.
- PEARL, RAYMOND. 1925. The Biology of Population Growth. New York (Alfred A. Knopf). Pp. 160.
- 1927. The growth of populations. *QUART. REV. BIOL.*, 2: pp. 532-548.
- 1928. The Rate of Living. Being an Account of Some Experimental Studies on the Biology of Life Duration. New York (Alfred A. Knopf). Pp. 185.
- 1932. The influence of density of population upon egg production in *Drosophila melanogaster*. *Jour. Exp. Zool.*, 63: pp. 57-84.
- , J. R. MINER, and S. L. PARKER. 1927. Experimental studies on the duration of life. XI. Density of population and life duration in *Drosophila*. *Amer. Nat.*, 61: pp. 289-318.
- , and S. L. PARKER. 1922. Experimental studies on the duration of life. IV. Data on the influence of density of population on the duration of life in *Drosophila*. *Amer. Nat.*, 56: pp. 312-321.
- , and W. B. D. PENNIMAN. 1926. Culture media for *Drosophila*. I. Changes in hydrogen ion concentration of the medium. *Ibid.*, 60: pp. 347-357.
- , and L. J. REED. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proc. Nat. Acad. Sci.*, 6: pp. 275-288.
- SMITH, HARRY S. 1935. The role of biotic factors in the determination of population densities. *Jour. Econ. Entom.*, 28: pp. 873-898.
- SPENCER, HERBERT. 1860. The social organism. *Westminster Rev.*, 73: pp. 90-121.
- STANLEY, JOHN. 1932. A mathematical theory of the growth of populations of the flour beetle, *Tribolium confusum*, Duv. *Canad. Jour. Res.*, 6: pp. 632-671.
- 1932a. A mathematical theory of the growth of populations of the flour beetle, *Tribolium confusum*, Duv. II. The distribution by ages in the early stages of population growth. *Ibid.*, 7: pp. 426-433.
- 1934. A mathematical theory of the growth of populations of the flour beetle, *Tribolium confusum*, Duv. III. The effect upon the early stages of population growth of changes in the nutritive value, palatability and density of packing of the flour medium. *Ibid.*, 11: pp. 728-732.
- 1938. The egg-producing capacity of populations of *Tribolium confusum* Duv. as affected by intensive cannibalistic egg-consumption. *Ibid.*, 16: pp. 300-306.
- THOMPSON, W. R. 1939. Biological control and the theories of interactions of populations. *Parasitology*, 31: (3); pp. 299-388.
- UVAROV, B. P. 1931. Insects and climate. *Trans. Roy. Ent. Soc. London*, 79: pp. 1-247.
- VLADIMEROVA, M. S., and E. S. SMIRNOV. 1938. The struggle for food in homogeneous and in mixed populations of *Musca domestica* and *Phormia groenlandica*. (With French summary.) *Meditsinskaja Parazitologija i Parazitarnye Bolezni (Med. Parasitol. and Parasitic Dis.)* 7: (5); pp. 755-777.

- VOLTERRA, VITO. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Accad. Naz. dei Lincei*, Series VI; Vol. 2.
- VOUTS, A. D. 1938. Bevolkingsproblemen I. De toename van een populatie van *Tribolium* en van de inheemsche bevolking van de Tenger. *Natuurkundig Tij. voor Nederl. Indis.*, pp. 163-167.
- WHEELER, W. M. 1913. *Ants*. New York (Columbia Univ. Press). Pp. 662.
- 1923. *Social Life among the Insects*. New York (Harcourt Brace). Pp. 375.
- 1928. *Emergent Evolution and the Development of Societies*. New York (Norton). Pp. 80.
- WIGGLESWORTH, V. B. 1939. *The Principles of Insect Physiology*. London (Methuen and Co.) Pp. 434.
- WILSON, E. B., and R. R. PUFFER. 1933. Least squares and laws of population growth. *Proc. Amer. Acad. Arts and Sci.*, 68: pp. 285-382.
- WINBOR, CHARLES P. 1937. Controlling factors in *Drosophila* population growth. *QUART. REV. BIOL.*, 12: (3); pp. 348-351.
- WRIGHT, SEWALL G. 1931. Evolution in Mendelian populations. *Genetics*, 16: pp. 97-159.
- 1935. The emergence of novelty. (Review of C. L. MORGAN.) *Jour. Heredity*, 26: (9); pp. 369-373.



AVIAN HOSTS FOR MALARIA RESEARCH

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INTRODUCTION

EXPERIMENTS with avian malaria have contributed a great deal to our understanding of the life cycle of the human malaria parasite. In addition, the basic studies on chemotherapy of malaria have been carried out with birds, and have resulted in the discovery of the two best known synthetic drugs, plasmochin and atabrin.

No existing antimalarial drugs, however, have proven to be completely satisfactory. Moreover, the supply in this country of quinine, plasmochin and atabrin has been threatened by the blockade of the second world war. For this reason, an intensive program has been established in search for a new antimalarial drug which could be produced domestically. Consequently, avian hosts are playing an increasingly important role in malaria research in the United States.

The purpose of the present paper is (1) to discuss the avian hosts of malarial parasites available for laboratory use, (2) to point out their advantages and disadvantages as tools in malaria research, (3) to provide some information concerning the supply and maintenance in the laboratory of the duck which the author believes to be the most suitable host at the present time, and (4) to list the contributions to our knowledge of the biology of *Plasmodium* resulting from the study of this parasite in different hosts.

Canary

More than 130 species of birds are known to be infected in nature with the malaria parasite, *Plasmodium* (Manwell and Herman, 1935). From these birds, more than a dozen accepted species of *Plasmodium* have been described. Early investigators used wild birds as experimental hosts for malaria research. However, the presence of natural infections in such hosts often interfered with their experiments. It was, therefore, necessary to obtain a domesticated host raised under conditions which would preclude the possibility of natural infection with *Plasmodium*. The canary satisfied this need when it was found to be susceptible to *Plasmodium* by Koch (1899) and others. Until recently, the canary has been used widely and almost exclusively as an experimental host for avian malaria studies. It was a suitable host not only because it proved to be susceptible to most of the known species of *Plasmodium*, but also because it could easily be maintained under laboratory conditions.

However, Laveran noted as early as 1891, that the usefulness of the canary as an experimental host for malaria research is limited by its small size. With the development of modern methods of research, particularly with the use of the Warburg apparatus, the limitation of the canary has become even more apparent. This bird usually can not provide more than one

cubic centimeter of blood even if it is exsanguinated. The need for an avian host which could supply a large volume of blood is imperative for many of the *in vitro* investigations on immunity, biology, chemotherapy and cultivation of *Plasmodium*. Moreover, the *in vivo* studies of the malaria parasite in canaries, may be complicated by the fact that in the preparation of films the daily blood losses may produce anemia in such a small host.

Aside from the small size, the usefulness of the canary as an experimental host is limited also by its high cost and inadequate supply due to the fact that it has not been bred in this country on a large scale. Female canaries, which do not sing, cost much less than male birds, but even they are expensive. Moreover, the price of canaries has been doubled, and in some localities, tripled by the present war blockage. According to Jaquith (1941), the import of canaries from Europe, usually amounting to 175,000 birds annually, has been completely discontinued since February 1940. As a result, the bird dealers are looking for substitutes to be used as pets.

For the reasons listed above, attempts have been made by various investigators in this country to secure a large and inexpensive experimental host for the study of avian malaria parasites. Chickens, pigeons, and ducks have been tested for this purpose with relatively successful results reported in 1938 by Coggeshall, Coatney, and Wolfson, respectively.

Chicken and pigeon

Manwell (1933) found that of the five well-known species of avian *Plasmodium* tested (*P. cathemerium*, *P. relictum*, *P. circumflexum*, *P. rouxi*, and *P. elongatum*), none survived in chicks for more than 10 days after inoculation. Temporary infections with *Plasmodium* in chickens have

also been reported by Coatney (1938) who used *P. relictum*, Wolfson (1940a) and Hegner and West (1941b) who used *P. cathemerium*. Brumpt (1935) described a new species of *Plasmodium*, *P. gallinaceum*, from a wild fowl of Ceylon, and later was able to maintain it in domestic fowls. A great deal of experimental work with *P. gallinaceum* has been reported from abroad, but this species is not available for study in the United States, since its import is prohibited by the quarantine law. More recently, Coggeshall (1938) successfully inoculated domestic baby chicks with another new species of *Plasmodium*, *P. lophurae*, which he isolated from a pheasant in the New York Zoological Garden. According to him, the number of parasites at the peak of infection may be high, but a large number of parasites in the inoculum is required in order to transmit the infection. For maintaining *P. lophurae* in the laboratory, frequent transmission from chick to chick is imperative. The inoculum must always consist of blood from an acute case, because the parasite can not be recovered from chicks during the latent period of the infection.

It has been generally believed that pigeons are not susceptible to laboratory strains of avian *Plasmodium*, since unsuccessful attempts to inoculate them were reported as early as 1899 and 1908 by Koch and Wasielewsky respectively. Wolfson (1937a) found that the wood thrush strain of *P. cathemerium*, generally maintained in canaries, produced an infection in pigeons which lasted for at least 46 days after the inoculation. Since then it has been learned by the author that although the number of parasites in the circulating blood of pigeons may be too low for a direct microscopic finding, pigeons harbor *P. cathemerium* for at least as long as one year and probably as long as they live. Several investigators, including Sergeants

(1904), Ogawa (1912), Böing (1925), and Coatney (1938), have observed plasmodia in natural infections of pigeons. Coatney succeeded in inoculating a strain of *P. relictum* from a naturally infected pigeon into other pigeons experimentally, and has since maintained it in the laboratory.

Thus *P. lophurae* of chicks and *P. relictum* of pigeons are available for study in large experimental hosts. However, these hosts have the following limitations: (1) each of the hosts is known to be susceptible to only one species of *Plasmodium* which precludes comparative studies of different species in the same host; (2) no satisfactory insect vector is known for either of the two species; (3) *P. lophurae* produces only a transitory infection in chickens; (4) pigeons can not feed themselves during the first three weeks after hatching. In order to prevent the possible infection of squabs with *Haemoproteus* while they are in the nests, special screened cages have to be used for breeding pigeons. This special set up raises their price almost to the level of that of the canary.

Duck

The first attempt to infect the duck with *Plasmodium* proved successful (Wolfson, 1938). The wood thrush strain of *P. cabanensis* which was inoculated into the duck at that time has been maintained since then in this host. Later, the duck was found to be susceptible to *P. relictum*, *P. lophurae*, and *P. elongatum* (Wolfson, 1939, and 1940b). As is the case with the canary, the susceptibility of the duck to the different species of *Plasmodium* is different in degree. Likewise, the rapid transmission of the parasite through the duck increases the duck's susceptibility. The course of the infection of the four species (five strains) of *Plasmodium* in the duck is summarised in Table 1. Most of the 250 ducks included in this table were of the

Pekin breed under 2 weeks of age (weighing less than 100 grams) at the time of the inoculation. No prepatent period occurred in infections with any species of *Plasmodium* after the intravenous inoculation with a large dose of parasites. When the doses were small, the prepatent period lasted up to one week after the inoculation. The length of the patent period was less than 2 weeks in all species with the exception of *P. lophurae*. In *P. lophurae* it lasted up to three weeks, but usually terminated in the death of the host before that time. The highest number of parasites in the circulating blood of the ducks at the peak of infection did not exceed 4,000 per 10,000 erythrocytes in three species. In *P. lophurae*, however, the number of parasites per 10,000 erythrocytes usually reached 10,000 and sometimes became as high as 19,000. The lowest number of parasites at the peak of infection was observed in *P. elongatum* and the maternal strain of *P. relictum*. In both of these, the number of parasites did not exceed 500 per 10,000 erythrocytes. In *P. elongatum*, at times more parasites were found in tissues, particularly the bone marrow, than in the circulating blood. Therefore, the number of parasites in the blood of birds infected with *P. elongatum* was not a true indication of the severity of this infection. It is clear from Table 1, that the susceptibility of the duck to *P. lophurae* is greater than to any other species thus far studied.

Further studies showed that the duck exhibits no age immunity to infection with *P. lophurae*. Table 2 illustrates the course of the infection in three ducks of different weights and ages which were inoculated simultaneously with an equal number of parasites per gram of weight. In the adult Pekin duck (6 months old), weighing 6.3 pounds (1750 grams), the number of parasites on the sixth day after the

inoculation reached the usual 10,000 per 10,000 erythrocytes. However, even when the infection was very high, for example in a Muscovy duck weighing 280 grams (Table 2), only 80 per cent of the red cells of the circulating blood were found to be infected, with each cell containing 3 to 4 parasites on an average.

after inoculation. At the end of these periods all ducks were still found to be infected. Occasional relapses several months after inoculation have been observed in ducks infected with *P. casthemerium*. However, no systematic study of relapses has been made.

Embryos

Unsuccessful attempts at cultivation of avian *Plasmodium* in egg embryos have been reported on several occasions. The first report on the subject is probably that of Huff and Bloom (1935) who injected canary embryo with *P. elongatum* "in order to determine whether the primitive blood cells and primitive erythroblasts should harbor these parasites." Similarly, negative results were obtained on three other occasions when *P. gallinaceum* of chickens was injected into chicken embryos (Gavrilov, Bobkoff, and Laurencin, 1938; Chorine, 1938; Rita, 1940). On the basis of these negative findings, Rita proposed a hypothesis that some fundamental changes must take place in the embryo at hatching, thus rendering the bird susceptible to *Plasmodium* to which it had not been susceptible before hatching. However, positive results of cultivation of *Plasmodium* in egg embryos published by other investigators tend to destroy the basis for this hypothesis.

Wolfson (1940b) reported successful cultivation of three species of *Plasmodium* in 14-day-old duck embryos inoculated with infected duck blood. In embryos infected with *P. casthemerium* no parasites were observed for 7 days after inoculation. Later a considerable number of them could be found in the blood. When blood films from a single embryo were studied on four different occasions, a few parasites were found on the 7th day after the inoculation, 500 parasites per 10,000 erythrocytes on the 8th day, 2,000 parasites per 10,000

TABLE 1
Four species of Plasmodium in ducks

SPECIES	NUMBER OF BIRDS USED	PATENT PERIOD IN WEEKS	HIGHEST PARASITE NUMBER PER 10,000 r.b.c.
<i>P. casthemerium</i> . . .	131	1-2	4,000
<i>P. relictrum</i>			
capistrani strain.	8	1 Or < 1	1,500
matinal strain.	60	1 Or < 1	500
<i>P. lophurae</i>	29	1-3*	19,000
<i>P. elongatum</i>	22	1	500

* Infection usually terminates in death of the host.

TABLE 2
Plasmodium lophurae in ducks of different weights

TIME AFTER INOCULATION	NUMBER OF PARASITES PER 10,000 RED BLOOD CELLS		
	1750 grams	580 grams	280 grams
30 minutes	100	160	120
12 hours	140	160	180
4 days	2,000	1,500	2,200
5 days	7,000	7,500	7,800
6 days	10,000	10,400	10,000
7 days	Dead	Killed	19,300
8 days	—	—	—
9 days	—	—	6,000
10 days	—	—	Dead

The duck exhibits definite age immunity to the other three species of *Plasmodium* studied. However, after recovery from an acute infection the duck seems to harbor the parasites as long as it lives. It has been possible to keep three ducks infected with *P. casthemerium* for at least one year after inoculation. One duck infected with *P. elongatum* has been kept for 10 months

erythrocytes on the 11th day, and 1,500 at death, on the 12th day. One embryo inoculated with *P. elongatum* was found to contain more than 3,000 parasites per 10,000 erythrocytes 7 days after inoculation. This exceeded several times the number found in the peripheral blood of ducks infected with this species. Duck embryos seemed to be less susceptible to *P. lophurae*. No parasites were found in the blood of embryos during 15 days after inoculation with large numbers of *P. lophurae*. However, a few parasites were observed at hatching. *P. cathemerium* prefers immature erythrocytes, whereas *P. lophurae* prefers mature cells. It is possible, therefore, that the degree of susceptibility of the duck embryo to the different species of *Plasmodium* is directly proportional to the degree of preference of the parasite for immature erythrocytes.

Shortt, Menon and Iyer (1940) successfully inoculated a 14-day-old chick embryo with sporozoites of *P. galinaceum*. At hatching, when the chicken was dead, a "moderate" infection was observed in the erythrocytes of its heart blood. In addition, a large number of exoerythrocytic stages were found in the liver, spleen, bone marrow, and particularly in the brain.

On the basis of the evidence existing at present, it may be concluded that at least three species of *Plasmodium*, *P. cathemerium*, *P. elongatum*, and *P. lophurae*, can be cultivated in duck embryos. Whether *P. gallinaceum* can be cultivated in chicken embryos by inoculation of infected blood is uncertain, but its cultivation can apparently be accomplished by inoculation of sporozoites.

Tissue culture

Huff and Bloom (1935), succeeded in maintaining *P. elongatum* in the culture of infected canary bone marrow for 48 hours, but *P. cathemerium* under the same condi-

tions gave negative results. Gavrillov, Bobkoff, and Laurencin (1938), reported a survival of *P. gallinaceum* for 10 days in culture of infected chicken bone marrow. Hegner and Wolfson (1939) were able to maintain the wood thrush strain of *P. cathemerium* in culture of canary lung and spleen for 8 days.

In recent unpublished experiments the author has been able to maintain the wood thrush strain of *P. cathemerium* in the lung culture of two canaries for 14 days each, and that of one duck for 7 days. In one of these canaries, exoerythrocytic stages were observed at autopsy, in the other canary (inoculated from a duck) and in the duck, no such stages could be found at autopsy.

Thus far, three species of *Plasmodium* have been successfully maintained in tissue cultures. *P. elongatum* in canary bone marrow (2 days), *P. gallinaceum* in chicken bone marrow (10 days), and the wood thrush strain of *P. cathemerium* in canary lung (14 days) and in duck lung (7 days).

Advantages of the duck over the canary, chicken, and pigeon

The duck, like the canary, is susceptible to several species of avian *Plasmodium*, each of which produces a sufficiently high and lasting infection to be useful in experimental work. The advantages of the duck over the canary are numerous. At the time of hatching the duck weighs more than twice as much as the adult canary, and provides proportionally more blood than does the latter. Since ducks can be obtained directly from the breeder immediately upon hatching, their age and history can be ascertained with ease and accuracy. It is usually impossible to determine the history of canaries because they (1) are not marketed for several months after hatching and (2) are usually sold by the dealers rather than by the original breeders. If necessary, the sex of

ducks can be determined, whereas the sex of canaries, if they do not sing, can be definitely established only at autopsy. Finally, there is an ample supply of ducks in this country and their cost is less than one quarter of the pre-war price of canaries.

The advantage of the duck over the chicken and pigeon lies partly in the fact that the duck is susceptible to more than one species of *Plasmodium*; besides, *P. lophurae*—the only available parasite of chickens—produces a much higher and more lasting infection in the duck than it does in the chicken. Age immunity to *P. lophurae* which is marked in the chicken does not exist in the duck. Furthermore, the leg vein of the duck is conspicuous, so that the parasites can be inoculated into it with ease. An additional advantage of the duck over the pigeon lies in the fact that, like the chicken, the duck can be secured immediately upon hatching and therefore is certain to be free from infection previous to experimental inoculation. The pigeon, on the other hand, can not feed itself for the first three weeks after hatching. While in the nest, it is exposed to infection with *Haemoproteus* and possibly *Plasmodium*. The breeding of pigeons in specially provided screened cages raises their cost to four times that of the ducks.

The problem of insect vectors of *Plasmodium* should also be considered. The final test of any antimalarial drug is its ability to cure, and particularly, to prevent infection which in nature is transmitted by the insect vector. It is, therefore, important to know the vectors of the laboratory strains of *Plasmodium*. Mosquito vectors are known for most of the well-established species of *Plasmodium* residing in canaries. No such vector is known at present for the strain maintained in the pigeon. Likewise, no satisfactory vector has been found for *P. lophurae* in

chickens. Laird (1941) found that *Aedes albopictus* fed on infected ducks developed sporozoites of *P. lophurae*. But these sporozoites inoculated into new ducks did not produce an infection as severe as is usually caused by the inoculation of trophozoites from the blood. The other three species of *Plasmodium*, known to infect ducks, are the same species and strains as have been studied in canaries, and their transmission has been accomplished on numerous occasions. *Culex pipiens* has been successfully used by the present author in transmission of the wood thrush strain of *P. cathemerium* and the capistrani strain of *P. relictum* (Wolfson, 1936, 1937b). *P. cathemerium* has also been transmitted by *Culex pipiens* from canary to duck (Wolfson, 1940a). Huff (1932) reported the susceptibility of several species of *Culex* mosquitoes and *Aedes triseriatus* to *P. elongatum*. Thus the mosquito vectors are known for at least three species of *Plasmodium* residing in the duck.

Finally, only the duck embryo was proven to be susceptible to the species of *Plasmodium* available for study in this country. *Plasmodium* can be maintained in cultures of duck tissue as well as in that of the canary.

Breeds and breeding seasons of ducks

The breeds of domestic ducks are discussed by Jull (1930) and Lee (1933, 1937). Of the 11 standard breeds existing, 10 are descended from the wild mallard (*Anas boschas*); the eleventh, the Muscovy, is sometimes considered to belong to a different species (*Anas moschata*). Only the Pekin breed of ducks is produced by the commercial duck farmers of the United States. The intensive commercial duck farming in this country began with the introduction of Pekin ducks from China in 1873. With very few exceptions, all the

Pekins in this country are descended from the original 20 ducks. This fact is responsible for their uniformity. The Pekins are hardy, timid, docile, and fair layers. Since they are non-sitters, their eggs are usually incubated artificially. The Muscovy ducks, infrequently bred by general farmers, are comparatively poor layers. Because of the difference in size of the duck and the drake, they are not as well suited for marketing. In addition, being good flyers, they can easily fly over ordinary poultry fences and therefore, are difficult to raise. The Pekin breed is, therefore, the most popular with commercial and general farmers.

The breeding season of ducks is adapted to the demands of the market and the convenience of the breeders. According to Lee (1933), on large commercial farms, ducks are hatched in the winter or early spring, forced for rapid growth, and marketed at 9-13 weeks of age. Ducks which are produced on general farms, are usually hatched in the spring and marketed in the fall or winter at the age of 5-7 months. The regular hatching season of ducks begins in December and extends through May and into June. A local general farmer, although breeding ducks on a small scale, has been able to provide young ducks and fertile eggs for this laboratory all the year round with the exception of the two autumn months, September and October. According to him, during that time the number of eggs layed by his flock was not large enough to make it profitable for him to run the incubator. But this year he increased his flock and therefore expects to have a supply of ducks all the year round.

The weights of ducks

According to Jull (1930), the following are the standard weights for the adult

ducks: Pekin duck = 8 lbs.; drake = 9 lbs.; Muscovy duck = 7 lbs.; drake = 10 lbs.

The weight changes in the growing ducks depend on the diet used and the amount of exercise allowed. Horton (1928) reported the weight changes of Pekin ducklings beginning with the egg at the time of incubation and ending with a 12-week-old duck. He gave the average weight of 2.01 ounces (35 grams) for ducklings when they hatched. His figures expressed in grams are as follows: At the end of 1st week = 44 gr.; 2nd week = 98 gr.; 3rd week = 227.5 gr.; 4th week = 401.5 gr.; 5th week = 560 gr., and so on. On the whole, normal ducks kept in the laboratory show similar changes in weight.

The blood picture of ducks

A thorough investigation of the normal blood of the domestic ducks was reported by Magath and Higgins in 1934. They were dealing probably with the Pekin breed of ducks referring to them as "tame mallard." Of eight ducks used by them, three were males and five females. The amount of hemoglobin was found to be 15.6 ± 0.35 gr. per 100 cc. of blood. The number of cells = $3,065,000 \pm 32,000$ per cubic millimeter. The length of the erythrocytes varied from 9.9 to 13.4 microns with 11.2 as an average; the width from 5.9 to 8.9 microns with 6.7 as an average. The values for the length and the width of the nucleus are 5 to 7 microns by 1.5 to 2.5 microns. The erythrocyte count is given as $3,065,000 \pm 32,000$, reticulocytes representing 20.7 ± 0.67 per cent. The leucocyte count was found to be $23,400 \pm 811$, of which 24.3 ± 0.33 were polymorphonuclear (with eosinophilic granules), 61.7 ± 0.41 lymphocytes, 10.8 ± 0.34 = monocytes, 1.5 ± 0.5 basophils. The mean thrombocyte number was computed to be 30.706 ± 703 .

Maintenance of ducks, duck embryos, and tissue cultures in the laboratory

The suitability of ducks as experimental animals is not generally known since they have not been used until recently. Several requests have been directed to this laboratory for information on how to take care of ducks, and particularly, how to provide water for swimming.

In this laboratory ducks have been used since 1938. Their maintenance does not require any provisions different from those used for chickens. For more than two years, the birds have been kept successfully in any type of cages available. These were usually old rat cages. Electric heaters placed near the cages provided the additional heat required by ducklings under two or three weeks of age. Regular brooders equipped with heating elements have also been used and have naturally been found to be more satisfactory. The daily care given to ducks consists in supplying them with drinking water and food (chicken mash). Several times a week the cages are thoroughly cleaned. Unlike the Muscovy, the Pekin ducks have a "quack" which is heard when they are hungry.

Ducks thrive without swimming, but they like to dip themselves in drinking water (as do canaries when supplied with drinking water in containers placed on the bottom of the cages). If wet and chilled, ducks develop pneumonia and die. Therefore water containers used for duck cages should be such as to prevent the birds from getting wet. Regular brooders eliminate this difficulty. Ducks should not be given ice cold water to drink, since it causes an acute indigestion and produces death within a few minutes. Common diarrhea may occur in ducklings at a very early age due to over-feeding, over-heating, chilling, or ice cold drinking water. To treat this condition, Hunter (1935)

suggests that the birds be given a teaspoonful of bicarbonate of soda to each quart of drinking water for one day. This treatment may be repeated after two or three days if necessary, but the pens should be thoroughly cleaned after each treatment. According to Hunter, the ducks are subject to very few of the many diseases common to most poultry.

Embryos of Pekin ducks have been successfully maintained in this laboratory at a temperature of 100 to 105 degrees Fahrenheit. The humidity in a 60-egg electric incubator fluctuated between 50 and 70 per cent. In addition, the eggs were dipped daily in lukewarm water. The incubation period of the Pekin duck egg (28 days) is one week longer than that of the chicken egg (21 days). Since the duck egg provides a longer period for the study of the parasites than does the chicken egg, the former is more desirable for the cultivation of *Plasmodium*.

Most of the tissue cultures of *Plasmodium* maintained in this laboratory were of the so-called "roller" tube type. The details of the technique used in preparation and maintenance of such cultures is given by Gey (1936). The essentials of such a technique can be summarized as follows. Small pieces of infected tissue are placed on the walls of the test tube and kept in position by coagulated plasma. Supernatant fluid added thereafter consists of balanced salt solution, embryo extract, and serum. This fluid provides nutritive material and is usually replaced every two or three days. The test tubes are held in a nearly horizontal position in a slowly rotating drum, and incubated at a temperature of 37.5 degrees centigrade. The rotation of the tubes causes the tissue to be intermittently bathed in the nutritive medium and exposed to the oxygen of the air.

So-called "hanging drop" cultures were

also used with a nutritive medium similar to that listed above.

Contributions to our knowledge of the biology of plasmodium by the study of parasites in different hosts

It is known that certain species of avian *Plasmodium* in canaries prefer reticulocytes to mature erythrocytes (Hegner and Eskridge, 1938). When some of these species of *Plasmodium* were inoculated into the duck, it was found that such preference persisted. This indicates that it is not due to the species of host harboring the parasite, but rather to the innate nature of the parasite itself. *P. cathemerium* and *P. relictum* in canaries as well as in ducks prefer immature erythrocytes, whereas *P. lophurae*, whether residing in the chick or in the duck, prefers mature erythrocytes.

Recently a new, exoerythrocytic, stage in the life cycle of the malaria parasite has been described from birds and was reported to occur in man. Exoerythrocytic stages found in association with all the species of avian *Plasmodium* except *P. elongatum*, are believed to represent an additional, perhaps "incidental," cycle independent from the erythrocytic cycle. Exoerythrocytic stages found in canaries infected with *P. elongatum* are believed to represent a part of the cycle in the red cells, and to be necessary rather than incidental for the persistence of the erythrocytic infection in this species (Parker and Huff, 1940). When *P. cathemerium* and *P. elongatum* were transmitted from canaries to ducks, it was found that the exoerythrocytic stages of *P. elongatum* persisted in the ducks, whereas the exoerythrocytic stages of the wood thrush strain of *P. cathemerium* which were always found in canaries apparently disappeared in the ducks (Wolfson, 1940a, b). Similarly, exoerythrocytic stages found in penguins infected with *P. relictum*

(Rodhain, 1938), disappeared when the infection was transmitted to canaries. Thus the presence of exoerythrocytic stages of avian *Plasmodium* other than *P. elongatum* depends on the species of host.

The basic criterion for the differentiation of the species of avian *Plasmodium* is morphology. When *P. cathemerium* and *P. relictum* were transmitted from canaries to ducks certain changes in the morphology of these parasites were observed (Wolfson, 1938, 1939; Hegner and West, 1941a). The effect of the host on the morphology of *Plasmodium* could not be determined previously when studies on the morphology of avian *Plasmodium* had been carried out with the canary as the only host.

In addition to changes in morphology, Hegner and West (1941b) noted a possible change in the length of the asexual cycle in *P. cathemerium*, from 24 hours in the canary to 48 hours in the chick.

The difference in the virulence of *Plasmodium* in different hosts is quite conspicuous. This fact has been used by the author in keeping certain strains in the laboratory in less susceptible hosts, to avoid the necessity of frequent transmission. For example, the wood thrush strain of *P. cathemerium* is very pathogenic for canaries. It kills the host usually within two weeks after inoculation. The author has kept this strain in a duck thus saving the trouble and the expense of transmission until such a time when it is needed for research in canaries. Similarly, the author has kept in canaries *P. lophurae* which kills ducks. In canaries the infection with *P. lophurae* is mild, but the author found it to last for at least 15 weeks.

It has been generally believed that the periodicity of *Plasmodium* depends upon

the diurnal changes in the environment of the parasite and the host, such as the intake of food, muscular activity, and temperature. Since the environment of the egg embryo is more constant and can be controlled much more readily than the environment of the bird after hatching, the study of the periodic phenomena of *Plasmodium* in the embryo presents certain advantages. It has thus far been observed that the residence of *Plasmodium* in the embryo tends to increase the synchronicity of segmentation of the parasite (Wolfson, 1940b).

Tissue cultures are useful in the study of the life cycle of *Plasmodium*. Hanging drop cultures which permit the observation of the living tissue under the microscope can be employed for the study of processes of multiplication and penetration of the parasite into new host cells. Since red cells do not multiply in cultures, whereas the cells containing the exoerythrocytic stages may undergo such multiplication, the "roller tube" tissue cultures have been employed for the purpose of studying the relationship between the erythrocytic and the exoerythrocytic stages of *Plasmodium*. Although the results obtained thus far are not conclusive, they seem to indicate that erythrocytic and exoerythrocytic stages can undergo a change from one to the other, in cultures, in the vertebrate host, or in both. Cultures of infected duck embryo tissues may prove to be more suitable for the study of *Plasmodium* than have been cultures of tissues from older birds.

SUMMARY

Of four avian hosts available for malaria research in the United States canary, chicken, pigeon, and duck, the duck is believed to be the most suitable.

(1) Like the canary, the duck is susceptible to several species of *Plasmodium*, each of which produces a sufficiently severe and lasting infection to be useful for laboratory study. The chief advantages of the duck over the canary are its large size, low cost and adequate supply.

(2) Unlike the duck, the chicken and pigeon are each susceptible only to one species of *Plasmodium* available in this country. Moreover, even *P. lophurae* produces a more severe and lasting infection in the duck than it does in the chicken.

(3) The vector of *Plasmodium* residing in the pigeon are unknown, whereas, the vectors of at least three species of *Plasmodium* residing in the duck are known.

(4) Only duck embryos are thus far known to be susceptible to species of *Plasmodium* available in this country.

(5) Pekin ducks are grown commercially in this country on a large scale. They can be bred throughout the year even on small general farms.

(6) The normal blood picture of ducks has been investigated and reported.

(7) The maintenance of ducks and duck embryos in the laboratory presents no difficulty. *Plasmodium* in duck tissues can be maintained successfully in culture.

(8) Contributions to our knowledge of the biology of *Plasmodium* by the study of the parasite in different avian hosts are numerous.

LIST OF LITERATURE

- | | |
|---|---|
| <p>BÖING, W. 1925. Untersuchungen über Blutschmarotzer bei einheimischem Vogelwild. <i>Centralbl. Bakter. Abt. 1. Orig.</i>, 95: 312-327.</p> | <p>BRUMPT, E. 1935. Paludism aviaire: <i>Plasmodium gallinaceum</i> n. sp. de la poule domestique. <i>C. R. Acad. Sci.</i>, 200: 783-785.</p> |
|---|---|

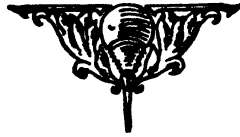
- CHORINE, V. 1938. Resistance de l'embryon de poulet à l'infection due au *Plasmodium gallinaceum*. *Ann. Inst. Pasteur*, 61: 829.
- COATNEY, G. R. 1938. A strain of *Plasmodium relictum* from doves and pigeons infective to canaries and the common fowl. *Amer. Jour. Hyg.*, 27: 380-389.
- COOPERHALL, L. T. 1938. *Plasmodium lepburae*, a new species of malaria parasite pathogenic for the domestic fowl. *Amer. Jour. Hyg.*, 27: 615-618.
- GAVERILOV, W., BOBKOFF, G., and LAURENCIN, S. 1938. Essai de en tissu de *Plasmodium gallinaceum* (Brumpt). *Ann. Soc. Belge de Med. Trop.*, 18: 429-434.
- GET, G. O., and GET, M. K. 1936. The maintenance of human normal cells and tumor cells in continuous cultures. *Amer. Jour. Cancer*, 27: 45-76.
- HENNER, R., and ESKRIDGE, L. 1938. Susceptibility of young red cells to the merozoites of avian plasmodia. *Amer. Jour. Hyg.*, 27: 471-492.
- , and WOLFSON, F. 1939. Tissue-culture studies of parasites in reticulo-endothelial cells in birds infected with *Plasmodium*. *Amer. Jour. Hyg.*, 29: (Sec. C) 83-39.
- , and WEST, E. 1941a. Modifications of *Plasmodium cathemerium* when transmitted from canaries to ducks. *Amer. Jour. Hyg.* 34: 27-39.
- , 1941b. Transmission of malaria parasite (*Plasmodium cathemerium*) from canaries and ducks to fowls, and their modification. *Amer. Jour. Hyg.* 34: 40-46.
- HORTON, H. D. 1928. The growth of white pekin ducklings. *Poultry Science*, 7: 163-167.
- HUFF, C. G. 1932. Further infectivity experiments with mosquitoes and bird malaria. *Amer. Jour. Hyg.*, 15: 751-754.
- , and BLOOM, W. 1935. A malarial parasite infecting all blood and blood-forming cells of birds. *Jour. Inf. Diseases*, 57: 315-336.
- HUNTER, J. M. 1935. Profitable duck management. Beacon Milling Co. Inc. Ceyoga, N. Y.
- JAQUITH, P. 1941. In place of canaries. *New York Times Magazine*, March 30, p. 10.
- JULL, M. A. 1930. Fowls of forest and stream tamed by man. *Nat. Geog. Magaz.*, 57: 327-371.
- KOCH, R. 1899. Über die Entwicklung der Malaria parasiten. *Zentralbl. f. Bakt. Parasit. u. Infektionsk.*, 121: 401-409.
- LAIRD, R. 1941. Studies on transmission of *P. lepburae* by mosquitoes. *Amer. Jour. Hyg.* (in press).
- LAVERAN, M. L. 1891. Des hematozoaires des oiseaux voisins de l'hématozoaire du paludisme. *C. R. Soc. Biol.*, 3: (mem.) 127-132.
- LEE, A. R., and MATTHEW, S. 1933. Duck raising. *U. S. Dept. Agric. Farmer's Bull.*, 697: 1-22.
- , 1937. Duck breeding. *Yearbook U. S. Dept. Agric.*, 1367-1378.
- MAGATH, T. B., and HIGGINS, G. M. 1934. The blood of normal ducks. *Folia Haematologica*, 51: 230-241.
- MANWELL, R. D. 1933. The behavior of the avian malaras in the common fowl, an abnormal host. *Amer. Jour. Trop. Med.*, 13: 98-111.
- , and HERMAN, C. 1935. The occurrence of the avian malaras in nature. *Amer. Jour. Trop. Med.*, 15: 661-673.
- OGAWA, M. 1912. Notizen über die blutparasitischen Protozoen bei japanischen Vögeln. *Arch. f. Protistk.*, 24: 119-126.
- PORTER, R. J., and HUFF, C. G. 1940. Review of literature on exo-erythrocytic schizogony in certain malarial parasites and its relation to the schizogonic cycle in *Plasmodium elongatum*. *Amer. Jour. Trop. Med.*, 10: 869-889.
- RITA, G. 1940. Tentativi de infezione dell'embrione di pollo con *Plasmodium gallinaceum*. *Riv. Mal.*, 19: 230-233.
- RODHAIN, J. 1938. Schizogony sans pigment chez un pingouin experimentalement infecte de *Plasmodium praecox (relictum)*. *C. R. Soc. Biol.*, 127: 838-840.
- SERGEANT, EDM., and SERGEANT, ET. 1904. Sur les Hematozoaires des Oiseaux d'Algerie. *C. R. Soc. Biol.*, 1: 132-122.
- SHORTT, H. E., MENON, K. P. and IYER, P. V. 1940. The form of *Plasmodium gallinaceum* present in the incubation period of the infection. *Ind. Jour. Med. Res.*, 18: 273-276.
- WASIELEWSKI, VON T. 1908. Pathogene Protozoen. *Leipzig*. Zweites Heft, p. 92.
- WOLFSON, F. 1936. Bird malaria transmitted by the intravenous injection of sporozoites. *Jour. Parasit.*, 22: 291-292.
- , 1937a. Experimental infections in owls and pigeons with *Plasmodium* of the wood thrush. *Amer. Jour. Hyg.*, 26: 53-59.
- , 1937b. Experimental transmission of Toxoplasma in canaries. *Jour. Parasit.*, 23: 553.
- , 1938. The common duck as a convenient experimental host for avian *Plasmodium*. *Amer. Jour. Hyg.*, 28: 317-320.
- , 1939. Morphological difference in *Plas-*

modium relictum in canaries and ducks (*Anas boschas domestica*). *Amer. Jour. Hyg.*, 30: 123-124.

—. 1940a. Exo-erythrocytic schizogony associated with the wood thrush strain of *Plasmodium*

catbemerium in relation to the species of the host. *Amer. Jour. Hyg.*, 31: (Sec. C) 26-35.

———. 1940b. Successful cultivation of avian *Plasmodium* in duck embryos. *Amer. Jour. Hyg.*, 32: (Sec. C) 60-61.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the contents, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of THE QUARTERLY REVIEW OF BIOLOGY, Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore, Maryland, U. S. A.

SOME NOTABLE ESSAYS ON PROTOZOAN RESEARCH

Being a review of *Protozoa in Biological Research*, edited by G. N. Calkins and F. M. Summers. New York (Columbia University Press), 1941. Pp. xli + 1148. 9 x 6. \$10.00.

By Willis H. Johnson, Department of Biology, Stanford University.

During the past century the "little animals" of Leeuwenhoek have figured prominently in biological researches throughout the world. Many students have studied the Protozoa simply to gain a better understanding of this group of organisms, but many more have used these forms in their researches as suitable material for the elucidation of general biological problems. This volume, according to the editors in their preface, is the result of "a discussion by a group of specialists assembled during the summer of 1937 at the Marine Biological Laboratory at Woods Hole, Massachusetts, for the purpose of ascertaining the best means to stimulate further research on these unicellular animals." If these organisms have turned out to be less "simple" than they were once considered to be, they are, and will continue to be, very useful organisms in the study of many biological problems.

The book contains twenty chapters written by as many recognized authorities in the field. The following list of authors and subjects will give a good idea of the

scope and nature of this work: G. N. Calkins, "General considerations"; H. W. Beams and R. L. King, "Some physical properties of the protoplasm of the Protozoa"; R. F. MacLennan, "Cytoplasmic inclusions"; C. V. Taylor, "Fibrillar systems in ciliates"; S. O. Mast, "Motor responses in unicellular animals"; T. L. Jahn, "Respiratory metabolism"; J. H. Weatherby, "The contractile vacuole"; G. W. Kidder, "The technique and significance of control in protozoan culture"; R. P. Hall, "Food requirements and other factors influencing growth of Protozoa"; O. W. Richards, "The growth of Protozoa"; C. A. Kofoed, "The life cycle of the Protozoa"; J. P. Turner, "Fertilization in Protozoa"; L. L. Woodruff, "Endomixis"; T. M. Sonneborn, "Sexuality in unicellular organisms"; H. S. Jennings, "Inheritance in Protozoa"; F. M. Summers, "The Protozoa in connection with morphogenetic problems"; E. R. Becker, "Certain aspects of pathogenicity in Protozoa"; W. H. Taliaferro, "The immunology of the parasitic Protozoa"; Harold Kirby, Jr., "Relationships between certain Protozoa and other animals" and "Organisms living on and in Protozoa".

In one group of chapters the nature of protoplasm, its organization and reorganization, is discussed from various angles. The introductory chapter contains brief discussions of the ecology of the Protozoa and of the history of protozoology, but the major discussion is concerned with

the problems of reorganization. Calkins speaks of a *fundamental organization* such as is found in a cyst or in an egg, characterized by undifferentiated protoplasm, and a *derived organization* which comes from the fundamental through metabolic activity and which is characteristic of the adult and all of its parts. The macronucleus, which is derived from the micronucleus, is described as the chief derived structure in ciliates. The renewal or reorganization of this important organelle is considered essential for continued vitality.

The authors of the second chapter state that while protozoan cells are the most highly differentiated of all cells, many of the differentiations are reversible. It should be added that in many of the Protozoa most of the differentiated structures are reversible. In this chapter a large number of researches dealing with the physical properties of protoplasm are reviewed. Such topics as the colloidal nature of protoplasm, surface properties, adhesiveness, density, optical properties, structural properties, and the effects of various agents on protoplasm are discussed.

A careful review of the diverse kinds of cytoplasmic inclusions which have been described in the Protozoa is given in the third chapter. A considerable confusion in the literature is indicated—a confusion in the names given to the different granules by different workers. These granules are difficult to classify either morphologically or on the basis of function. Many of these inclusions have counterparts in metazoan cells (mitochondria, Golgi bodies, etc.). The author takes the stand that these inclusions are formed "de novo" in the cells, that they are visible products of chemical reactions which occur in the cells. He states that "the cell is not restricted in the accomplishment of its functions by any system of universal and invariable cytoplasmic components".

The nature of fibrillar systems, parts of the derived organization, as known in four typical ciliates, *Paramecium*, *Stentor*, *Euplores*, and *Vorticella*, is clearly outlined in Chapter IV. A survey of a number of other forms is given and the differences in the interpretations of the various workers is considered. In conclusion, Taylor, a

pioneer student in this field, points out that some of the elements described may belong to the pellicle and that the fibrillar structures vary in function in different organisms, functioning in contractility in some, in conduction in some, and possibly in support in some.

The chapter on contractile vacuoles contains discussions of the origin, the structure and the function of these organelles. As described, contractile vacuoles form as a result of the activity of certain formed inclusions. In the formation of temporary vacuoles small vacuoles fuse; in permanent vacuoles droplets enter filling canals. The evidence on the function of these vacuoles is conflicting. Evidence is presented which indicates that they are organelles which prevent excessive dilution of the cytoplasm. It is also suggested that they may play a rôle in excretion.

The chapter on motor responses in unicellular animals is in many ways closely related to those just referred to. That the sol-gel, gel-sol changes which occur in the locomotion of an amoeba are tied up closely with the protoplasmic organization of the amoeba is recognized. That a clear understanding of the physical changes in the protoplasm involved in such movements is not yet at hand is indicated in this discussion. In this chapter Mast gives detailed discussions of the more recent investigations concerning the motor responses of the rhizopods, flagellates, ciliates and colonial forms to light, electricity, and chemicals.

Students interested in the general problem of growth will find the discussions in Chapters VI, VIII, IX, and X interesting. In Chapter VIII the various methods of sterilizing Protozoa are described in detail. The author rightly emphasizes the need for rigid bacteriological methods in pure culture studies and the need for standardization of the nutrients employed. Attention is called to the difficulties encountered in attempts to culture certain organisms in pure culture because they apparently require something from living sources. In this connection the problem of growth factors and vitamins in protozoan cultures is raised. As pointed out here, recent studies show that a number of substances act as growth factors or as growth stimu-

lants for certain unicellular organisms. The literature reviewed on this point indicates that this is a fertile field for future investigations.

A simplified classification of the Protozoa, based on their carbon and nitrogen requirements, is presented in Chapter IX. It is hoped that the classification outlined here will come into common usage. In this chapter the effects of the concentration of nutrients, the hydrogen ion concentration, the oxygen content, the redox potential, temperature and light on growth are discussed and many unsolved problems are pointed out. Population growth curves are discussed in both Chapters IX and X. A need for more detailed studies with pure cultures is indicated.

In a definition of growth the author of Chapter X states, "Growth is a fundamental attribute of living organisms, manifested by a change of size of the individual, or in the number of organisms in a unit of environment". It is gratifying to see the inclusion of the second part of this definition because usage justifies it. Many writers, however, have insisted that growth pertains only to an increase in size of the individual. Interesting methods of making counts and of measuring the volume of unicellular organisms are discussed in this chapter. It is suggested that the old problem of allelocatalysis should be reinvestigated using motion pictures, on the theory that the effect may be due to more swimming when the organisms are in large volumes of media.

The problem of growth is intimately related to the problem of respiratory metabolism. A well-written discussion of the general problem of respiratory metabolism and an attempt to link the general subject to protozoan work is found in Chapter VI. That relatively little work has been done on the subject is indicated by the author when he states, "it seems probable that in the near future we shall see the development of an organized account of protozoan respiration, and it also appears that this investigation will take place among investigators who are primarily interested in the Protozoa". The author paves the way for this work by (1) outlining and discussing the known methods of measuring aerobic respiration,

(2) suggesting problems for solution in connection with a discussion of the effects of various substances on oxygen consumption, and (3) outlining the theories on the mechanism of respiration.

The chapters on the life cycle, fertilization, endomixis, sexuality, and inheritance are closely related. In Chapter XI, Kofoed, a veteran student of life cycles in the Protozoa, discusses two types of cycles. In one type, characteristic of primitive forms, there is an alternation of binary and multiple fission; in the other type there is an alternation of sexual and asexual reproduction. Attention is called to the fact that although sexual reproduction is not found among the primitive Protozoa it has evolved in this group and is characteristic of the higher Protozoa. The life cycles of the higher Protozoa, as of the Metazoa, include maturation, fertilization, cleavage, histogenesis, sexual dimorphism and gametogenesis. The emphasis placed on the unicellular nature of the Protozoa, according to the author, "tends to obscure their basic similarity in life cycle to that of the Metazoa, and thus to minimize the biological significances of the varied evolutionary accomplishments which have occurred in this primitive phylum".

A discussion of fertilization, as a part of the life cycle, is continued in Chapter XII. Numerous examples, illustrating copulation, autogamy and conjugation, are described. Such questions as, what is the real nature of the life cycle of the common amoeba, what is the rôle of the macronucleus in conjugation, are nuclei derived from chromidia, and numerous others, will suggest to readers of this chapter many problems for future research. In the following chapter, Chapter XIII, a clear discussion of the reorganization of the macronucleus in the Ciliophora, in intrinsic reorganization, in endomixis, in autogamy and in conjugation is presented. Woodruff questions Diller's conclusion that endomixis does not exist and presents evidence that both autogamy and endomixis occur in *Paramecium*. The facts presented here indicate that complete information on the nature of reorganization in *Paramecium* must await further research.

The discussion of sexuality, in Chapter

XIV, is based primarily on two genera, *Chlamydomonas* and *Paramecium*. The discussion of *Chlamydomonas* constitutes a good review of the numerous publications of Moewus on this genus. As is indicated here, Moewus has reduced what appeared to be a multiple sex system in this genus, through chemical analysis, to a dual system (male and female). Certain inconsistencies are pointed out in the work of Moewus. Because of the numerous criticisms which have been directed against these studies on *Chlamydomonas* the author of this chapter rightly suggests that this work is in urgent need of repetition. The discussion of sexuality in *Paramecium* is in part based on the author's own careful studies. The systems of mating types, as worked out for several species, are outlined and discussed. The author argues for a "multiple sex" system in ciliates rather than for a "male and female" system. Two kinds of copulation-conditioning factors are suggested: one functioning in bringing cells together, the other functioning in bringing together their nuclei.

Inheritance in the Protozoa is discussed in Chapter XV under the headings, uniparental inheritance, biparental inheritance in haploids, and biparental inheritance in diploids. In the treatment of biparental inheritance in haploids the researches of Moewus on flagellates are further reviewed. Jennings, the author of this chapter, cites examples from Moewus' studies which show that independent assortment, linkage, crossing over, sex linkage and sex inheritance occur in these organisms. He states that this work of Moewus has placed the genetics of Protozoa on a new footing; but at the same time he points out that Moewus' conclusion on crossing over, which is based on two-strand crossing over, is a serious difficulty and needs clearing up. The discussion of biparental inheritance in diploids is based on the work of Sonneborn, Jennings and their associates on *Paramecium*. It is shown that segregation of the diverse mating types takes place at the first fission following conjugation. Most of the clones are like one of the two parent types, but a few are different, unlike either parent type. The author states that, so far, this situation is unexplained. The discussion,

here, of the relative rôles of cytoplasm and nucleus in inheritance is quite interesting. As a rule, in uniparental inheritance, racial or inherited characteristics are not altered; but Jennings points out that there are exceptions. Among such exceptions are the cases of degenerative changes resulting from unfavorable conditions which are inherited for long periods and cases of acclimation to chemicals and heat (Jollos' *Dauermodifikationen*) which may be inherited for hundreds of generations. The results of De Garis on size inheritance in *Paramecium* are compared with these cases. De Garis found that when individuals from a large race and a very small race conjugate, the offspring are like the parents for a number of generations, but after from 20 to 30 generations the nuclei exert their influences and the offspring have a common size. The effects of the cytoplasm in this case are of much shorter duration than in those described by Jollos. The author concludes that "the question whether inherited environmental modifications are exclusively cytoplasmic, or whether they affect the chromosomal material of the nucleus, must be left open for the present." However, the clear-cut experiment which he outlines to resolve this question will surely be carried out in the near future.

In the chapter on morphogenesis the rôles of various factors such as the external environment, stage in the life cycle, conjugation, encystment, degree of injury, size of fragments, and nuclei on regenerative processes are considered. Numerous interesting problems are suggested. This chapter, dealing as it does with the fundamental organization of protozoan protoplasm, might have been placed more logically with some of the earlier chapters.

The general nature of pathogenicity in the Protozoa is discussed in Chapter XVII. The author considers that the use of the three categories, commensals, symbionts and pathogenes, is highly artificial because there are no counterparts in the zoological scheme for these categories—there are no classes, orders, families or genera which have as their distinguishing character that they are pathogenic. In a discussion of several studies on *Endamoeba bistolytica* and on *Plasmodium vivax* the author stresses the fact that within a given

species there are strains which vary greatly in their pathogenicity. This situation plus the great variation in the resistance of hosts to invading organisms are presented as primary considerations for investigators in this field.

In the following chapter an excellent and extensive account of protozoan immunity is presented. A description of the cellular and serological mechanisms of the host in protozoan immunity is followed by detailed discussions of immunity in malaria and in trypanosome infections. Taliaferro indicates that little success has been attained with artificial immunization in protozoan work. However, a number of useful tests which aid in diagnosis are described.

The relationships of Protozoa and other animals, usually considered under the categories of symbiosis, commensalism and parasitism, are discussed in Chapter XIX. Kirby prefers to refer to all of these relationships as symbiosis because the term, symbiosis, was so used originally by de Bary. Many cases of accidental and facultative parasitism are reviewed. The case of *Glaucoma*, which is used so much in laboratory studies and which has been found as a facultative parasite in several kinds of animals, is an interesting one. The evolutionary developments presented in the discussion of systematically related free-living and symbiotic flagellates and ciliates are quite instructive. Among the other subjects treated in this chapter are the question of host-specificity in connection with distributional host relationships, adaptations for attachment and for completion of the life cycle and the nature of the obligatory mutualism which exists with termites and their faunas of Protozoa. Kirby also contributed the last chapter which deals with parasites in Protozoa. This chapter will be interesting to many readers. Many cases of parasitism involv-

ing bacteria, fungi, and other protozoans are discussed. The author points out that these parasites of Protozoa have resulted in much confusion in the literature because they have been described by different workers as pellicular striations, supernumerary flagella, cilia and mitochondria. It is clearly indicated in this discussion that much remains to be done in this field.

When considered as a whole the book is well written. A few of the chapters are rather tedious to read largely because the authors, in their attempts to cover the literature in their fields, present page after page of abstracted material. In the preface the editors state that "our first real difficulty was to select a limited number of topics from a vast number of possibilities." To the reviewer it seems that only two serious omissions were made. Because so much emphasis is placed, and rightly so, on the organization and reorganization of the protoplasm of Protozoa in the first few chapters, a chapter on encystment and excystment, if included, would have made possible a more complete treatment of this subject. Also, since these unicellular organisms are so important in the general economy of nature, a chapter on the ecology of the Protozoa would have added to the value of the book.

This series of discussions will not only stimulate further research on the Protozoa but it will also facilitate such work in many ways. In most of the chapters a fairly thorough review of the literature, especially the recent literature, is given and in most instances the studies reviewed are evaluated and correlated. In each chapter literally dozens of problems for future investigation are outlined or suggested. For all workers in the field, and especially for beginning investigators, the very extensive bibliographies at the ends of the chapters will be quite useful. Wherever Protozoa are studied this volume will be invaluable for years to come.

BRIEF NOTICES

EVOLUTION

THE UPPER TRIASSIC FLORA OF ARIZONA.
With a Discussion of Its Geologic Occurrence,
by Howard R. Stagner. Contributions

to Paleontology. Carnegie Institution of
Washington Publication No. 526.

By Lyman H. Daugherty. Carnegie Institution of Washington, Washington, D. C.

\$1.75 (cloth); \$1.25 (paper). 11½ x 9; iii + 108 + 34 plates; 1941.

Stagner states that the leaf shales of the Blue Forest occur "below or interfingered with the less massive phases of the Newspaper Rock sandstone. . . . The field characteristics of these beds suggest deposition in a stream channel or estuary. The differences in composition, distribution, and structure of the bentonitic beds suggest a different mode of deposition for them," possibly lacustrine or subaerial deposits of volcanic ash.

The collections were made largely within the Petrified Forest National Monument near Holbrook, Arizona. The flora is represented by 6 classes, 11 orders, 35 genera, and 38 species, the dominant members being cycads and the Osmundaceae, the largest family of ferns. Descriptions are given of these different forms, and in a series of fine plates are shown the characteristic features. Preceding the descriptions there is a section on the topography, climate, and vegetation of this region at the present time and of conditions during the Upper Triassic. A list of 86 references and an index are provided.



WHEN THE WORLD WAS YOUNG.

By *Martha McBride Morrel*. Houghton Mifflin Company, Boston. \$3.00. 8½ x 5½; xvi + 252; 1941

The origin and history of the earth with all its endowments and adornments has long fired man's imagination and curiosity, and tested his patience, skill, and ingenuity in piecing together the fragmentary fossil records of its past. The work of the archaeologist and the geologist has been richly rewarded, in that we now have a fairly clear idea of the age of the earth, as well as numerous activities, both animate and inanimate, that have occurred on or in the earth since its birth.

In a delightfully simple style, the author has incorporated into this fascinating book many scientifically accurate facts concerning the origin of the earth and the origin and evolution of life upon the earth. No attempt is made to include detailed and documentary evidence of

these facts. Rather, the whole topic is developed in story fashion, and is written in language understandable to everyone. A bibliography and an index are provided.



GENETICS

HANDBUCH DER ERBKRAKHEITEN. Band 2: *Die Schizophrenie*, by *Berthold Kihn* and *Hans Luxenburger*. Band 3: *Die erbliche Fallsucht; Der Erbveitstanz (Huntingtonsche Chorea); Der schwere Alkoholismus*, by *Klaus Conrad*, *J. L. Entres*, *Ferdinand A. Kehr*, *Friedrich Meggendorfer*, and *Kurt Poblisch*.

Edited by *Arthur Gütt*. Georg Thieme Verlag, Leipzig. Each volume: RM. 19.50 (cloth); RM. 18.00 (paper) (outside of Germany). [For subscribers to set of 6 volumes price reduced to RM. 18.00 (cloth); RM. 16.50 (paper).] 9½ x 6½; Bd. 2: viii + 336; Bd. 3: x + 454; 1940.

The preoccupation of the Nazi political philosophy with racism has given a great impetus to studies on human genetics. However, as has been sometimes the case with reference to the Eugenics movement, the investigations reported have been characterized by an enthusiastic desire to pass to immediate positive action rather than to contribute definitive knowledge about the biological foundations of diseases. These two volumes illustrate to some degree this attitude. For each of the conditions discussed, a section is devoted to the consideration of the legal measures that have been or could be adopted to outbreed it, for the purpose, of course, of improving the well being and health of the race. Volume 2 of this series concerns schizophrenia. In the first section Kihn describes in great detail, following accepted lines, the clinical manifestations and course of the disease, and evaluates the effects of the newer therapies advocated. Luxenburger reviews the data on the familial concentration of schizophrenia and schizoid personality. He brings out the difficulties in attempting to state psychic status of the relatives of schizophrenes or schizoids. He notes especially the discrepancies in the familial incidence rates reported by some

authors (he has limited himself to German data). While accepting the view that the disease or diseases grouped under the term schizophrenia have an inherited constitutional basis the author does not definitely assume that the hereditary transmission follows a particular Mendelian mechanism. A similar conclusion can be attributed to Conrad who, in Volume III, studied the hereditary factor in epilepsy. For this disease Pohlisch describes the clinical and pathological manifestations in great detail. Of especial interest is the attempt by both authors to classify what are the clinical and pathological traits that differentiate the several types of epilepsy discussed in the literature. In this same volume Huntington's chorea is discussed from the clinical standpoint by Kehrer and from the genetic side by Entres. In their respective sections these authors present a full and detailed review of the information available about this disease but add nothing new to the existing knowledge. Also in this volume Meggendorfer examines data from the literature, as well as his own, on the medical, pathological and genetic aspects of alcoholism. This is one of the most extensive summaries of the knowledge on the subject that has appeared. The author concludes, contrary to the opinion of many, that alcoholism is disgenic and consequently harmful to the race.

The exhaustive treatment of the several subjects included in these volumes, superior to other works so far published on diseases and inheritance, makes this series of *Handbücher* useful even though the occasional references to views we associate with the Nazi ideals will be distasteful to many. In addition, one criticism to be made is the inadequacy of the bibliography consulted and mentioned.



GENERAL BIOLOGY

WILLIAM BYRD'S NATURAL HISTORY OF VIRGINIA or *The Newly Discovered Eden*. Edited and Translated from a German Version by Richmond C. Beatty and William

J. Mulloy. *The Dietz Press, Richmond, Virginia*, \$4.00 9 x 5½; xxviii + 109; 1940.

This work, originally printed in German in Bern, Switzerland, in 1737 "at the command of the Helvetic Society", was written to interest the Swiss in the colonization of America—specifically the tract of 180,000 acres in Virginia owned by William Byrd, the founder of Richmond. Byrd was interested in bringing over Swiss settlers primarily as a check to the Catholic French and secondly to promote diversified farming to break the one crop obsession of the English settlers in Virginia which he feared would lead to economic distress. Incidentally, it appears that Jenner's group (Jenner was the translator of Byrd's description of Virginia into German) was the only one to accept Byrd's invitation. This

Description of Virginia, its climate, inhabitants, government, religious matters and religions, trade, cattle raising, price of provisions, as also of the species of money, fertility, fruits and vegetables, trees, uncultivated as well as cultivated, as also all sorts of species of plants, flowers, herbs and roots; likewise what sorts of wild and domesticated animals, fowls, as well as fish, crayfish and other animals are to be found in the land mentioned . . .

is an interesting addition to early Americana. We quote at random:

Buffalo is an animal with a hump on its back, of an enormous and terrible size, has long curly hair, from which the Indians make many things, and Europeans mattresses. . . . The meat and fat from it are as good as that from our oxen, indeed probably better. One has also *foxes* in this land. They are grey, but do not smell as bad as the European variety. One may obtain splendid wine from Madeira (a Canary Island), which is very delicious, and also strong, and which is far better and more healthful than all our European wines, not only because of its agreeable sweetness but because of its soothing quality, as I myself have found out.



CONSERVATION OF RENEWABLE NATURAL RESOURCES. *Some Fundamental Aspects of the Problem*. University of Pennsylvania Bicentennial Conference.

By Raphael Zon, William S. Cooper, Gustav A. Pearson et al. University of Pennsylvania Press, Philadelphia \$2.50. 9 x 5½; vi + 200; 1941.

It is encouraging to note that conserva-

tion of our nation's resources is finally attaining a position of importance. From this series of papers by men in responsible government agencies, in institutions, and in other positions concerned with the problem, it is evident that the nation is cognizant of its responsibility to the future. The trial and error methods of the pioneers, with the ruthless policies of waste and indifference, are past, and now that the country is suffering from this ravaging the time is ripe for constructive efforts.

These papers are limited to the plant world and the topics are divided into three main categories: first, the use of natural vegetation as a guide to agricultural and forestry practice; second, climatic cycles in relation to the theory and practice of conservation; and third, the administrative task of conservation.

Grasslands, prairies, soil, and streams have never attained the major rôle in our broader conservation measures that the forests and wild animals have attained. That they are fundamental to any policy of conservation (not merely in the sense of preservation) and that agriculture should work in conjunction with, rather than destructively against, these plant communities is the keynote of the first subgroup of topics. Following papers deal with solar cycles, dendro-chronology, climatic pulsations, etc., and their bearing directly or indirectly on conservation. The final section contains papers dealing with the responsibilities of the States and of the Federal Government with regard to this problem. Together, these papers form an important and reassuring contribution toward saner and better methods for the preservation of our natural resources.



MARINE PRODUCTS OF COMMERCE. *Their Acquisition, Handling, Biological Aspects and the Science and Technology of Their Preparation and Preservation.*

By Donald K. Tressler, in Collaboration with Ward T. Bower, E.D. Clark, et al. Reinhold Publishing Corporation, New York. \$12.00. 9 x 5½; 762; 1940.

A reprint (unchanged) of a volume which first appeared in 1923. In spite of its economic aspect the book contains much useful material for the biologist, and especially for the biochemist. Within its covers is gathered a great deal of information that can only be found elsewhere by referring to many different sources.

Several of the early chapters are devoted to marine salt, iodine, potash, algae, agar-agar, and alginic acid. Then follow sections on pearls, corals, characteristics of marine fishes, fish and liver oils, the shell fish, turtles and terrapins, whales, seals, walruses, and sponges. Aside from these subjects being treated from the commercial point of view there is a great deal on the life history, habitat and population of marine forms, their chemical properties, food value, etc. Lists of references conclude each chapter, and there are 257 figures and 90 numbered and many brief unnumbered tables in the text. In Appendix I are tables showing the statistics of the fisheries in the United States, by states; and in Appendix II is given a list of the common names (with descriptions) of the marine fish and animals of commercial importance of the United States and Alaska. An author index and a detailed subject index conclude the volume.



BIOLOGY WORKBOOK.

By B. B. Vance, C. A. Barker, and D. F. Miller. Edited by W. R. Teeters. J. B. Lippincott Company, Philadelphia. 92 cents. 10½ x 7; iv + 316; 1941 (paper). This high school manual is designed to make the pupil independent of constant direction, and provides an integrated problem-solving and comprehensive test program intended to fit the interests, needs, and abilities of the average student. It may be used with any standard textbook in high school biology, and specific page references to twenty of the commonly used high school texts in biology are listed at the beginning of each unit. Employing the unit-problem organization of subject matter, the work-book is organized into thirteen units. Each of these is divided into unit-problems which serve as the basis for student's classroom study, discussion,

and laboratory work. Included are projects, hobbies, field trips, extra assignments, outside readings, reports and other pupil activities. All activities point toward the practical side of science instruction. The order in which the units are arranged can readily be changed to suit the individual instructor, and enough material has been included for a complete school year. The book is profusely illustrated with well-chosen photographs and line drawings. There is no index.



GENERAL BIOLOGY. *Revised Edition.*

By James W. Mavor. *The Macmillan Company, New York.* \$4.00. $9\frac{1}{2}$ x 6; xxx + 897; 1941.

The present edition of this text largely overcomes the criticisms directed at the first edition (cf. Q.R.B., vol. 12, p. 92). The author has inserted at the end of most chapters a list of references specific to the preceding discussion. Although the original illustrations have been supplemented by a number of new and distinctive photographs, the volume still remains below par in this respect. Further major changes are the inclusion of a discussion of ecology, the addition of new material on the physiology of vertebrates, and revision of descriptions concerning the life cycle of plants. There has been slight change in the final section, which remains an excellent discussion of general biological principles. Having lost none of its original clarity and good organization, this book by its revision has been raised above the ranks of the average fundamental biological text. It contains appendices giving phylogenetic surveys of the plant and animal kingdoms and a detailed index.



BIOLOGICAL SYMPOSIA, Volume II. *Speciation. Defense Mechanisms in Plants and Animals. Biological Basis of Social Problems. Regeneration.*

Edited by Jacques Cattell. With a Foreword by George A. Baitsell. *Jacques Cattell Press, Lancaster, Pennsylvania.* \$2.50. $9\frac{1}{2}$ x $6\frac{1}{4}$; [8 unnumbered] + 270; 1941.

The species problem today appears, as it has in former years, to hold the master key to evolution. Until early in the present century the greatest handicap to biologists was the lack of knowledge of the details of the relationship of one generation to another. This relationship is now emerging with the rapid advances of genetic and cytological research. It is with this problem of speciation, influenced by modern research, that this first symposium of the series deals.

The second symposium is on the defense mechanisms present in plants and animals. The third treats of the biological basis of social problems and the fourth and last is on regeneration. The bibliography following each paper, although short, is well selected and will serve as a guide to further reading on the problem discussed.



FOUNDATIONS OF BIOLOGY. *Sixth Edition*

By Lorande L. Woodruff. *The Macmillan Company, New York.* \$3.75. $8\frac{3}{8}$ x $5\frac{1}{2}$; xvii + 773; 1941.

This sixth edition of Woodruff's fine text has been thoroughly revised. Material has been added to all chapters, especially those on plant structure and function, and animal coordination and development. Endocrinal coordination has been assigned a separate chapter and a chapter on human ancestry has been added.

The fundamental problems of biology embracing the large problem of life common to both zoology and botany, are brought together in brief form. The author believes that the general biological viewpoint is the most favorable means of approach, both to a broad knowledge of living phenomena as part of a liberal education and to more advanced studies in zoology and botany.



BIOLOGY AT THE UNIVERSITY OF RICHMOND.

By John W. Bailey. *University of Richmond, Richmond, Virginia.* \$2.50. 9 x $5\frac{1}{2}$; 194; 1939.

In this interesting little volume, the present head of the Biology Department of the

University of Richmond has recounted all the activities of the department from the time of its inception in 1903 to the time the book was written in 1939. The growth of the department from one instructor and a half-dozen students to the present staff of three full-time professors and six student assistants, and an annual enrollment of over fifty students is indicative of sound growth under able leadership.

The author's habit of keeping detailed records of the activities of his department has resulted in a volume that will be welcomed by alumni and friends of the University of Richmond.



NATURE NOTES.

By John Kieran. Doubleday, Doran and Co., New York. \$1.50. 7½ x 5; 112; 1941. Not an intensive study but short anecdotes to each topic contained in his book briefly sums up John Kieran's Nature Notes. Kieran lovingly presents his friends to the unscientific as well as to those better versed in nature lore. To those who study nature and nature's creatures these essays furnish delightful reading, and those who just admire birds and flowers for the pleasure they afford the eyes will appreciate them more after reading this collection by radio's famed mental encyclopaedia.



HUMAN BIOLOGY

LIFE AND LETTERS OF VASCO NÚÑEZ DE BALBOA including *The Conquest and Settlement of Darien and Panama, The Odyssey of the Discovery of the South Sea, A Description of the Splendid Armada to Castilla del Oro, and The Execution of the Adelantado at Acla.*

By Charles L. G. Anderson. Introduction by Ricardo J. Alfaro. Fleming H. Revell Company, New York, London and Edinburgh. \$3.50. 8½ x 5½; 368 + 2 folding maps; 1941.

The conquistadores were on the whole a bad lot. Cortés, the libertine and uxoricide, was surpassed in cruelty and treachery by Ojeda, Ovando, and the illiterate Pizarro, so that today the memory of these men is hated by the mestizo and they are

repudiated by the creole. Consequently it is refreshing to read in these pages of one who, although severe, was always just, and who recognized the claim of the aboriginal caciques to a rank equal to his own, who never forgot that he was their guest, and who always kept faith with them.

Concerning the early life of Vasco Núñez de Balboa nothing is known. Except for his participation in the Bastidos expedition his first appearance in history was when he stepped out of a cask in which he had been hiding as a stowaway on board a vessel carrying supplies from Española to the mainland. At that time he was 37 years old. At the age of 44 he was beheaded on a fake charge of treason, the result of the jealousy of the perfidious Pedrarias.

In those seven short years he had not only stood "silent upon a peak in Darien," beholding a new sea, more vast in extent than any body of water that had ever before met the gaze of a white man's eye, but also had established the first permanent settlement of Europeans in Veragua, as America was then called, had brought back the first account of the empire ruled by the Incas, had rescued two expeditions from disaster, and had finally been appointed leader of one of these, not by imperial fiat, but by the votes of those who had become his partners in adventure. If anything further is needed to convince the reader that Balboa was several centuries ahead of his time, let him imagine the fate that today would meet the crew of even a civil expedition, to say nothing of a military one, who should resort to the democratic procedure of choosing their officers by popular vote.

Among those executed with Balboa was his companion Hernando de Argüello. Was this man by any chance the ancestor of the family that supplied governors of California not only under the vice regency of New Spain but also under the empire of Iturbide, and whose most celebrated member was Srita. Concepcion de Argüello, the heroine of the poem by Bret Harte? It is the unexpected occurrence of such names as this that have already acquired historic and literary connotations that lend a peculiar fascination to the study of history.

A tremendous amount of scholarly re-

search has gone into the compilation of this book, and the author is to be congratulated on having made such a significant contribution to the early history and settlement of the continent upon which we live. Among the numerous plates is an illustration of the famous "White Indians" of Panama.



THE TRUTH ABOUT LEIF ERICSSON AND THE GREENLAND VOYAGES.

By William B. Goodwin. Meador Publishing Company, Boston. \$3.50. 9½ x 5½; 445; 1941.

The author tells us that this book is the culmination of over thirty years study. The reader who finishes it is likely to put it down with the feeling that if he could have devoted so long a time to the study of one subject, he could have produced a much more convincing argument.

The author's thesis is that the site of Vinland of the sagas was the present Portsmouth Harbor, New Hampshire, and it may well be that it was, but the liberal use of such words as "if," "probably," and "provided that" which are generously sprinkled over the narrative tend to weaken the force of the argument and to beget doubts in the mind of the reader from Missouri (why does the author refer to Kentucky as the home of skeptic critics?). The author is also addicted to the etymologically hybrid word "mapographer." Cartographer is the generally accepted term. He also uses the ambiguous expression "and/or," a device to which recourse is had by shallow thinkers who are uncertain which of the two words expresses their meaning. It is borrowed from jurisprudence and has no place in a scientific work.

The most original feature of the book is a discussion of some rather mysterious stone foundations in the interior of New England which the author has been investigating. According to the sagas the Norse settlers always remained close to the shore, and these stone buildings must have been the work of another people. Among the Norsemen themselves was a tradition that in a still earlier period there were settlements in Vinland older than their own,

which they attributed to Irish colonists. Celtic-speaking aborigines, supposed to be the descendants of these early settlers, figure prominently in the sagas, and to these people the author suspects the stone foundations to be due, but has not as yet made a sufficiently detailed study to justify his conclusions.

The Norse settlement is perhaps the most fascinating and romantic chapter in American history, and a scholarly work dealing with what is known of it, elucidating the sources of information, and expounding the various theories advanced by different authorities, would fill a long felt need. But the present work, which incidentally has no index, no bibliography, and no documentation, only bears witness to a muffed opportunity.



THE INDIANS OF THE WESTERN GREAT LAKES 1615-1760. *Occasional contributions from the Museum of Anthropology of the University of Michigan No. 10.*

By W. Vernon Kintz. University of Michigan Press, Ann Arbor. \$4.00 (cloth); \$3.50 (paper). 6 x 6½; xiv + 427; 1940.

This survey, based largely upon the material in the archives of Ottawa, Montreal, Chicago, Detroit, Ann Arbor, and Washington, D. C., but including also some material already published, contains much that is of interest concerning Indian tribes of the Great Lakes region at a period when they were not greatly disturbed by the presence of the white people. The beginning date, 1615, marks the time when the first explorers came in contact with a Michigan tribe, between Ottawa and Champlain on the eastern or northern shore of Georgian Bay, in 1615. Actually there was little contact with the Indians—aside from the Hurons who came to Michigan in 1650—before 1660, so that the material is largely a record from the year 1660 through the following one hundred years. The closing date of the survey, 1760, marks the capitulation of Canada by the French. Since the French were not especially interested in settling the land, and disturbed the Indians very little, the presence of the whites was not actually resented by the

Indian tribes until after the French lost control of the region.

Most of the material that Kinietz has collected has been taken from accounts by Frenchmen—missionaries, traders, and administrative officers—and concerns the following tribes: Huron, Miami, Ottawa, Potawtomi, and Chippewa. For each tribe there is much data on location, characteristics, dress and ornament, economic life, social life, and religion. Since, however, the records were left by people who were not writing for the historian, we are not furnished with well-rounded accounts on any one phase of Indian life, as the author points out. But the volume furnishes the student of ethnology and anthropology with much valuable material.

A scholarly work, well documented. In an appendix—Memoir concerning the different Indian Nations of North America, by Antoine Denis Raudot—will be found 45 letters translated from the French, the earlier ones dated around 1709-10, the later ones without dates. A detailed index is provided.



WINONA AND RIDGE RUIN. *Part I. Architecture and Material Culture.* Museum of Northern Arizona Bulletin 18.

By John C. McGregor. *Plant Materials* by Volney H. Jones. *Skeletal Material* by Katharine Bartlett. Northern Arizona Society of Science and Art, Flagstaff, Arizona. \$5.25 (cloth); \$4.75 (paper). 8½ x 5; 313, 1941.

WINONA AND RIDGE RUIN. *Part II. Notes on the Technology and Taxonomy of the Pottery.* Museum of Northern Arizona Bulletin 19.

By Harold S. Colson. Northern Arizona Society of Science and Art, Flagstaff, Arizona. \$1.75. 8½ x 5; 75; 1941 (paper).

For the past twelve years, the members of the staff of the Museum have been studying the archaeology of the region about the San Francisco Peaks in the north central part of Arizona. Previous publications have dealt with stages of the history before 1000 A.D. The present study deals with foci contemporary with late Pueblo II and early Pueblo III of the Anasazi chro-

nology, and carries the history to the period 1150-1200 A.D. It is concerned with an area of six square miles north and east of Winona Station, on the A.T. and Santa Fe Railroad, which presents a sample of the conditions to be found on the 800 square miles of the black sand area east of Flagstaff, if the whole area were studied intensively. The following subjects are discussed in order: dates, cultural stages, methods, pottery structures, ground and chipped stone, shell, bone and horn, basketry, textiles and wooden objects, food and other raw materials, and disposal of the dead. It is the firm belief of the writer that the ecology of the Winona-Ridge Ruin section was much different when occupied prehistorically than at present. The book is well illustrated and contains a complete bibliography and index.

In outlining prehistorical cultures in time and space, the archaeologist in the Southwest leans heavily on pottery for his clues, and Part II of this report is a careful and authoritative study of certain aspects of the ceramic technology of the Winona pottery. The author emphasizes that his present paper is but a report of progress made to date and is not to be considered as a complete study. Numerous helpful illustrations have been provided and a bibliography and index are appended to the volume.



GERTRUDE BELL.

By Ronald Bodley and Lorna Hearst. *The Macmillan Company, New York.* \$2.50. 8½ x 5½; x + 260; 1940.

This biography of the remarkable Gertrude Bell makes extremely interesting reading. Born, in 1868, and reared in a Victorian world when the lives of English girls of the upper classes followed very rigidly a conventional pattern, Gertrude Bell chose, at the age of 17, to go up to Oxford. There she passed all her examinations with distinction and took a "brilliant first class in modern history." Then followed a period in the social life of her class where her beauty and interesting personality gave her an unusual position. Traveling in the Orient she met Henry Cadogan who had a profound influence on

her life. Under the direction of Cadogen, to whom she became engaged but owing to his early death never married, she commenced the study of Persian and Arabic. The year 1899 marked the beginning of her journeys in the desert. After a few expeditions covering the beaten tracks until she had become proficient with her Arabic, she set off with her own caravan. The fine work that she did in archaeology and topography in the years preceding the first World War gave her a high rank among explorers and brought her many honors.

During the war Gertrude Bell's labors were in quite another field. Her keen understanding of the Oriental mind and the strong ties of friendship which she had formed with powerful tribal leaders as well as with nomads of lesser importance made it possible for her to render valuable aid to the British Intelligence Service. Lawrence, although of a younger generation, was her devoted friend and worked with her during these years. Later she became Political Secretary of the Mesopotamian Government and had an important part in establishing the kingdom of Iraq and in making Prince Feisal of Hejaz king. With the lessening of the heavy responsibilities in the English service Gertrude Bell turned again to travel, to archaeology, and to the building up of the Baghdad Museum. Her death in 1926 in her adopted country brought consternation and grief to the desert people who had come to regard her as their most valued friend in their relations with the British Government.



FAMILY AND COMMUNITY IN IRELAND.

By Conrad M. Arensberg and Solon T. Kimball. *Harvard University Press, Cambridge.*

\$3.50. 9½ x 6; xxix + 322; 1940.

One of the most curious and at the same time significant commentaries on the present status of the social sciences is that more precise information is available about the customs and social behavior of African or Australian natives than about the groups which comprise our civilization. It is, therefore, small wonder that the uplifter and others of like breed have to date been unable to formulate an effective program of social progress. Being well aware of this,

the authors have chosen to examine the social life and organization of County Clare in Ireland where they lived for two years or more. The observations on the familial, social and economic aspects of the people of this Irish county are here reported in detail and constitute the substance of the book. The impersonal and consequently objective evaluation of the social behavior of this Irish population brings out certain characteristics that reveal the multiplicity and complexity of the elements involved. The findings reveal that the social behavior of the population studied centers around, and is a function of, the family and community life particular to it. The contribution of these two institutions furnishes the broad directives of the mode of living of the individuals whose behavior is further determined by the social interactions that emerge from the relationships of (a) familialistic order, (b) age grading or generation, (c) sex organization, (d) local division of labor, (e) economic exchange. The demographic characteristics of the group result from the combined action of these variables. It may seem that no new light has been shed on the social characteristics of our civilization by the enumeration of the factors presumably involved, because the authors cannot as yet arrive at a quantitative measure of their respective influence. Nevertheless, the guiding idea behind this investigation and the analytical procedure employed represent a considerable advance in the methodology of social sciences.



FAMILY HOUSING AND FACILITIES: *Five Regions.* U. S. Department of Agriculture Miscellaneous Publication No. 399. *Consumer Purchases Study. Urban, Village, and Farm.*

By Hazel Kyrk, Day Monroe, Maryland Y. Pennell, and Edith Dyer Rainborb. *Government Printing Office, Washington, D. C.* 25 cents. 9½ x 5½; vi + 223; 1940 (paper).

FAMILY EXPENDITURES FOR MEDICAL CARE. *Five Regions.* U. S. Department of Agriculture Miscellaneous Publication No. 402. *Consumer Purchases Study. Urban, Village, and Farm.*

By Helen Hollingsworth, Day Monroe, Margaret C. Klem, and Karl L. Benson. Government Printing Office, Washington. 30 cents. 9½ x 5½; vi + 241; 1941 (paper).

FAMILY EXPENDITURES FOR AUTOMOBILE AND OTHER TRANSPORTATION. Five Regions. U. S. Department of Agriculture Miscellaneous Publication No. 415. Consumer Purchases Study. Urban, Village, and Farm.

By Day Monroe, Dorothy S. Brady, June F. Constantine, and Karl L. Benson. Government Printing Office, Washington. 30 cents. 9½ x 5½; iii + 272; 1941 (paper).

The housing conditions—number of rooms, facilities for water, heat and light, and sanitary conveniences—of families living in 20 small cities, 140 villages, and 64 counties of 12 farming sections of the United States are described in the first of these volumes. The second and third present data on expenditures for medical care and transportation, respectively, of families at different income levels in these same localities. All three are part of a survey made by the U. S. Bureau of Home Economics concerning the income and consumption patterns in five regions (New England, Middle Atlantic and North Central, Plains and Mountain, Pacific, and Southeast). Except for the Southeastern region for which Negro families are included, these reports are confined to families in which both husband and wife were native-born whites.



DRUMS AND SHADOWS. Survival Studies among the Georgia Coastal Negroes.

By the Savannah Unit, Georgia Writers' Project, Work Projects Administration. Foreword by Guy B. Johnson. Photographs by Muriel and Malcolm Bell, Jr. University of Georgia Press, Athens. \$3.00. 9½ x 5½; xx + 274 + 24 plates; 1940.

This is the report of a survey of the beliefs and superstitions of Negroes living on the coast and sea islands of Georgia. Over 130 Negroes (including one named Cohen) in 21 communities were interviewed and their beliefs regarding conjurers, witches, spirits, etc. were elicited. The exact formulation of the questions asked is not given here but the replies of the interviewed and their reactions are described in some detail.

The replies phonetically reproduced in the style and language of the interviewed constitute the substance of the book. Apparently, as the subtitle and preface indicate, the objective of the survey was to determine what residues of native African superstitions are still present in the American Negro. The person responsible for the elaboration of the data has evaded the issue by not discussing the superstitions but refers only to the parallelisms recorded by students of African lore. Numerous parallelisms are uncovered, and so, taking the findings at face value one could assume that certain beliefs have persisted after three generations in contact with the European civilization of our country. On the other hand, some of the superstitions of the African natives are common to European peoples. It follows that the findings reported here will need further interpretation before their significance regarding the survival of customs can be properly evaluated.



THE INTEGRATION OF AMERICAN SOCIETY. A Study of Groups and Institutions. First Edition.

By Robert C. Angell. McGraw-Hill Book Co., New York. \$2.50. 9 x 6; ix + 228; 1941.

The central question discussed in this book is whether or not the principal social groups into which our society can be differentiated are stable. That is, do they develop loyalty in the components of the group or express ultimate common values of American life? With this question in mind the author considers the organization and function of each of the following seven types of groups: capitalistic enterprises, struggle groups (labor unions, for example), governmental units, benevolent groups, families, churches, clubs, and associations. From the examination of these groups, Angell finds that their evolution to their present status has led them away from the local community. Few seem to stimulate concern for the common welfare, individual rather than common goals are emphasized, and agreement on the objectives for common action are not achieved. Therefore, the author believes that unless

the trend is checked it may lead to a complete disintegration of our society. As a remedy he suggests actions that will insure the persistence of our stock of common values and that will foster an increased understanding between the groups. Obviously the social evolution of the past century has altered the conditions which enter into some forms of social behavior. But are these changed conditions harmful for our society and social way of living? The evidence discussed does not really permit an answer to the question. Nor can a satisfactory answer be obtained without an elaborate analysis that takes into account the biological foundations of social intercourse, employs precise terminology, and is supported by factual evidence.



THE PLAINS INDIANS AND NEW MEXICO, 1751-1778. *A Collection of Documents Illustrative of the History of the Eastern Frontier of New Mexico.*

By Alfred B. Thomas. University of New Mexico Press, Albuquerque. \$3.50. 10½ x 6½; xv + 232; 1940.

The history of New Mexico from the time of its first pioneers to the middle of the nineteenth century was, with few exceptions, a continuous record of suffering on the part of the settlers from attacks by the Plains Indians—the Apaches, Comanches, Utes, Jumáños and Pawnees. Although much has been written on the relations between the Spaniards and the Pueblo Indians, who were easily subdued (there was only one Pueblo revolt), little attention has so far been paid to the rôle the Plains Indians played in retarding the colonization of New Mexico. From 1751 to 1778 the scene was dominated by two persons. Don Thomas Vélez Capuchín, Spanish governor from 1751 to 1767, and Medineta, who governed from 1767 to 1778. The former succeeded in establishing peaceful relations between the Pueblos, colonizers and the warring tribes. His policy included the halting of French trade which had hitherto supplied the Plains tribes with guns and powder, establishing trade relations between the Spaniards and Indians, and threatening one tribe against another. Medineta reverted to the ear-

lier policies of organizing expeditions and raids against the Plains Indians in an effort to subjugate them. The major portion of this book consists of translations of the policies and reports to their governmental superiors by these two governors. The introduction of 59 pages, a survey of the frontier history of New Mexico, offers a background for these reports. The book is profusely annotated, and is equipped with a bibliography and an index.



SOCIAL ORGANIZATION OF THE GĀ PEOPLE.

By M. J. Field. *Crown Agents for the Colonies, London.* 12s. 6d. 8½ x 5½; xiii + 231; 1940.

The Native Administrative Ordinance of the British Government was based upon the customs and needs of certain of the Gold Coast Colonies. It assumes that all of the natives can be governed by dealing through the chiefs of the tribes. When the ordinance was formulated it was not recognized that the Gā customs were essentially different from those of the other groups, and that they had no centralization of power. The attempt to remold the age-old Gā traditions to conform to the relatively new administrative policy has led only to destruction of order.

To assure an understanding of the difficulties involved, the writer has gone into considerable detail about the history and social organization of the Gā people. He describes first the customs which are common to the group as a whole, and second, how each town is an independent republic having its own peculiar organization. The book will command the interest of cultural anthropologists and, more important, of the administrators of colonial policy. The need for careful study of a people before formulating a plan for their government is strikingly presented.



MAN STANDS ALONE.

By Julian S. Huxley. *Harper and Brothers, New York and London.* \$2.75. 8½ x 5½; x + 297; 1941.

Fifteen pertinent essays, written at various times between 1927 and 1939 and all pre-

viously published in various periodicals, comprise this volume by the well-known biologist and humanist. They present a continuity of style and of method. The author himself sees the unity of the essays in the fact that they were written in "that strange restless indecisive period during which an age was dying, but most of us were refusing to face the imminence of its dissolution." Huxley sees before him and the world the task of the formulation of a social basis for civilization on the foundations of a new world picture reflecting special biological knowledge of the human being in all his uniqueness. Titles of the essays are: The uniqueness of man; Eugenics and society; Climate and human history; The concept of race; The size of living things; The origins of species; Mice and men; The way of the dodo; The courtship of animals; The intelligence of birds; Science, natural and social; The analysis of fame; Scientific humanism; Religion as an objective problem; and Life can be worth living. Thoughtful readers will doubtless challenge many of Huxley's inferences and conclusions, but they will also find his discussions interesting, instructive, and stimulating.



I WAS A HEAD-HUNTER.

By Lewis V. Cummings. Houghton Mifflin Co., Boston. \$3.00. 8 x 5½; ix + 338; 1941.

Starting from Bogota the author travelled alone across the mountains to a tributary of the Orinoco, the Guaviare River in Colombia. There he joined a primitive tribe of head-hunting Indians, learned their mode of existence and married three of their girls. He participated in their warfare, hunting, travels, and tribal ceremonies. The report of his adventures is entertainingly written and contains much information on the habits of these remote Indians and of the local game animals. Detailed notes and a glossary are added.



UNIVERSITY OF COLORADO STUDIES. Series B. *Studies in the Humanities*, Volume 1, Number 3. Containing the Following Ar-

ticles: *The First Biography of an English Poet*, by Irene P. McKeehan; *Germanic Influence on Old French Syntax*, by Paul-Louis Faye; *An Unnoticed Abridgment of the Historia de Preliis (Redaction I²-I³)*, by S. Harrison Thomson; *A Noteworthy Contribution to the Study of Bede*, by Jack D. A. Ogilvy; *George of Poděbrady and Bohemia to the Pacification of Silesia—1459*, by Otakar Odložilík; *The Leadership of the English Delegation at Constance*, by Allen duP. Breck; *Emperor Charles IV and Pope Innocent VI*, by Edwin J. Westermann; *AOI: Another Suggestion*, by Paul-Louis Faye.

University of Colorado, Boulder. \$1.00. 10 x 6½; 86; 1941 (paper).

ENGINEERING PROGRESS AND THE SOCIAL ORDER. University of Pennsylvania Bicentennial Conference, N-B.

By Frank B. Jewett and Robert W. King. University of Pennsylvania Press, Philadelphia. 25 cents. 9 x 6; 15; 1941 (paper).



ZOOLOGY

BRITISH GRAHAM LAND EXPEDITION 1934-37 SCIENTIFIC REPORTS. Volume 1. No. 1, *The Biology of the Weddell and Crabeater Seals with a Study of the Comparative Behaviour of the Pennipedia*, by G. C. L. Bertram; No. 2, *The Life Cycle of Wilson's Petrel Oceanites oceanicus (Kuhl)*, by Brian Roberts; No. 3, *The Breeding Behaviour of Penguins, with Special Reference to Pygoscelis papua (Forster)*, by Brian Roberts; No. 4, *On Two New Species of the Hydroid Myriotetha*, by S. M. Manton; No. 5, *Anoplura*, by Theresa Clay; No. 6, *Lower Crustacea*, by J. P. Harding; No. 7, *Sphaeroceridae (Diptera)*, by O. W. Richards.

The British Museum (Natural History), London. No. 1: 15s., No. 2: 7s. 6d., No. 3: 5s., No. 4: 5s., No. 5: 2s. 6d., No. 6: 1s., No. 7: 1s. 12½ x 9; No. 1: 1-139, No. 2: 141-194, No. 3: 195-254, No. 4: 255-294, No. 5: 295-318, No. 6: 319-322, No. 7: 323-326; Nos. 1-5, 1940, Nos. 6-7, 1941 (paper).

Important contributions to the knowledge of antarctic fauna are contained in this series. Bertram states, in his study of the Weddell and Crabeater seals (42 text-figures, 10 plates), that 367 of the former

and 177 of the latter were killed to provide food for the expedition, and that mostly the killing was in his hands. Conditions were rarely ideal for the complete examination of the bodies. Nevertheless the author succeeded in collecting a large amount of material bearing on the biology of these two species, the most abundant of the four species of Antarctic Phocids. Detailed studies were made on age, growth of fetuses and pups, skull development, and the ovaries. The report includes a section on the comparative behavior of the Pinnipedia, and in an addendum Bertram has arranged in condensed form, on a large folding chart, the main biological features of all the species of seals.

The second of these reports (24 text figures, 7 plates) gives much information on the taxonomy, breeding habits, migration, growth, etc. of Wilson's Petrel. The observations on breeding habits were made largely on a single colony, consisting of 23 nests in patches of moss. This colony was visited daily and the birds banded, the complete breeding cycle being covered for two seasons.

Limitation of space will permit only the mention of one other report in this series—The breeding behavior of Penguins (26 text figures, 4 plates)—which is the first of a series of studies on the Penguin data collected on this expedition. It is concerned chiefly with the Gentoo Penguin (*Pygoscelis papua*) and aims at "furthering knowledge of the responses which birds make to external (exteroceptive) and internal (proprioceptive) stimulation. The known facts about the characteristic behaviour phases of the breeding season are discussed in relation to recent advances in endocrinology." There is evidence that a "close correspondence exists between the cycle of internal changes in the mature bird and the sequence of activities which it is able to perform."

All of the studies in Volume I contain detailed reference lists.



THE LUNGFISH AND THE UNICORN. *An Excursion into Romantic Zoology.*

By Willy Ley. *Modern Age Books*, New York. \$2.75. 8½ x 5½; 305; 1941.

The subtitle of this work tells one exactly what to expect when we read it, and the reader will not be disappointed.

Prior to the period which the historians designate as the Renaissance of Learning the acquisition of knowledge came about solely by the authoritarian method. The result was that error was accumulated along with truth. In the field of zoology a great body of folk-lore grew up in this way, which for lack of a better name might be called *Parazöology*. The popular superstition that elephants are afraid of mice, or that horse-hairs turn into snakes if immersed in water, are excellent examples of this sort of material, which is not unworthy of serious study, for it throws light on the cerebration of human beings in past ages. Such figments of the imagination as the unicorn, the dragon, and the basilisk are full of interest and romance, and after reading about them in this book the reader is likely to regret that the author did not include as well the sphinx and the centaur, the mermaid and the werewolf, the cockatrice and the manticore.

The second part of the book deals with animals that within historic times have become extinct, or nearly so—the native European cattle, the great auk, and the dodo. (Incidentally, the author makes no mention of the fresco of the last named bird on the wall of the monastery of Saint Catherine, which antedates the discovery of it by the Portuguese in the sixteenth century by upwards of a thousand years.) The present reviewer must confess that before he read this book he did not know the difference between an aurochs and a wisent. The author has a delightful literary style that allows him to change the subject as often as he pleases, which he does by making digressions to discuss the quagga, the Arctic manatee, the passenger pigeon, and the gigantic ratite birds of Madagascar and New Zealand, all of which disappeared only quite recently.

Finally, there is a discussion of living fossils—those peculiar forms that are the last surviving representatives of groups that belong to the past—the horse-shoe crab, the duck-billed platypus, the lungfish, and the peculiar lizards from the southern hemisphere with functional pineal eyes. That most romantic of all

living fossils, the chambered nautilus, has been overlooked, but this omission can easily be forgiven in view of the delightful entertainment the author has given us.



THE MIGRATIONS OF ANIMALS FROM SEA TO LAND.

By A. S. Pearse. *Duke University Press, Durham, North Carolina.* \$3.00. 8½ x 5½; x + 176; 1936.

This is a well-written work on an important phase of ecology—the modifications which animals undergo when their environment is altered. The bibliography of 44 finely printed pages bears eloquent testimony to the painstaking research that has gone into its making. Yet it is not merely a digest of the printed reports of other people's work. The author himself has travelled extensively on four continents gathering material and checking up on the statements of others.

In the Cambridge Natural History published about half a century ago, the statement is made that many marine animals of the Indian Ocean have so adapted themselves to a fluviatile existence that they may be found in the Ganges river a thousand miles from the sea. The present author denies this statement, listing some of the same species by name, which he says have established themselves in the Ganges estuary, but are nowhere found in the river.

The work suffers from one serious defect—lack of proof-reading. A page inserted after the printing was done lists thirteen errata, mostly errors in spelling. The present reviewer has detected seventeen more, making a total of 30 in a book of only 186 pages. These are not all misspellings of scientific terms; many are the names of authorities quoted which are spelled one way in the text and another way in the bibliography. There is an old proverb that what is worth doing at all is worth doing well, and it may be that some readers may feel that since this book was not worth doing well it may not be worth reading. The reviewer would like to assure such readers that this book is really much better than its orthography would seem to indicate.

THE FISHES OF AUSTRALIA. Part I. The Sharks, Rays, Devil-Fish, and other Primitive Fishes of Australia and New Zealand.

By Gilbert P. Whitley. *Royal Zoological Society of New South Wales, Sydney.* 7s. 6d. 9½ x 6; 280; 1940.

This handbook is the first volume on the fishes of Australia and comprises the sharks and rays, as well as the lancelets, lampreys, and lungfishes. Succeeding volumes will consider the bony fishes.

Over one hundred species of these animals are listed and described, and nearly every form considered is illustrated by photographs or original drawings. The few facts known concerning the animal's life history, its range, and its relationship to man along with a more detailed and technical analysis for identification, are some of the topics discussed for each species. The writer has taken great pains to unearth many records of sharks attacking humans, and from a lengthy list of more or less substantiated records, he concludes that some species of sharks do attack men voluntarily and are not so harmless as some naturalists have claimed.

Other interesting topics such as an historical account of sharks, introduction to their anatomy, and especially an illustrated series of egg cases, all make this book a valuable contribution to a fascinating branch of ichthyology. Many myths are exploded, but facts stranger than fiction replace them. In view of the fact that sharks and rays assume a prominent position in the layman's mind, this book is recommended for authoritative information both from a scientific and a popular viewpoint.



THE AUDUBON GUIDE TO ATTRACTING BIRDS.

Edited by John H. Baker. *Doubleday, Doran and Co., New York.* \$2.50. 7½ x 5½; xviii + 268; 1941.

Almost all of the conceivable ways to attract birds and to provide for them are to be found in the chapters written by Roger T. Peterson, Richard H. Pough, John H. Baker, and Dorothy Treat that go to make up this guide for bird lovers. After preliminary chapters on bird study, photog-

raphy, and banding, Peterson explains how planting, artificial feeding, nesting boxes, and water can attract various species of birds and how these can be utilized in the most advantageous manner. Feeding birds consists of more than merely throwing bread crumbs on the ground, and providing nesting sites is more than knocking together any old kind of bird box. Consequently all those desirous of attracting birds—school teachers, home owners, or ornithologists—should first read this book and profit by the numerous suggestions and directions that it contains.

Wisely, there is a chapter on predators, and then to complete the book and enhance its value, there are sections on trespassing, maintenance of sanctuaries, bird attraction as an educational community project, and the individual's rôle in the protection of wildlife.



ZOOLOGICA. *Scientific Contributions of the New York Zoological Society. Volume XXVI, Part 1, Numbers 1-12.*

New York Zoological Society. Zoological Park, New York. \$2.00. 10½ x 7; 64 + 12 plates; 1941 (paper).

This number contains the following papers:

A new crayfish from San Luis Potosí, Mexico. (Decapoda, Astacidae), by Horton H. Hobbs, Jr. (1 text-figure); A new *Corydoras* from Brazil, by F. R. Lamonte; Notes on plumage changes in the Bald Eagle, by Lee S. Crandall (4 plates); External characters of six embryo nurse sharks, *Ginglymostoma cirratum* (Gmelin), by William Beebe (2 plates; 4 text-figures); A papillomatous disease of the gallbladder associated with infection by flukes, occurring in the marine turtle, *Chelonia mydas* (Linnaeus), by G. M. Smith, C. W. Coates, and R. F. Nigrelli (4 plates; 1 text-figure); Eastern Pacific Expeditions of the New York Zoological Society, XXIII. Polychaetous annelids from the west coast of Mexico and Central America, by Aaron L. Treadwell (21 text-figures); Plankton of the Bermuda Oceanographic Expeditions. X. Polychaetous annelids from Bermuda plankton, with eight shore species, and four from Haiti, by Aaron L. Treadwell (9 text-figures); Caudal skeleton of Bermuda shallow water fishes. V. Order Percomorphi: Carangidae, by Gloria Hollister (20 text-figures); Description of an egg of the Long-tailed Bird of Paradise, by Lee S. Crandall (1 plate); On the uterine young of *Dasyatis sabinus* (Le Sueur) and *Dasyatis hastatus* (De Kay), by C. M. Breder, Jr., and Louis A. Krumholz (2 text-figures); Additional social and physiological aspects of respiratory behavior in small tarpon, by Arthur Schlaifer; Notes on Mexican snakes of the genus *Trimorphosaurus*, by Hobart M. Smith.

INTRODUCTION TO GENERAL ZOOLOGY.

By Nathan Fasten. Ginn and Company, Boston. \$3.75. 9½ x 5½; viii + 742; 1941.

A new text for an elementary course in general zoology that is destined to find a useful place in the teaching of this subject. The author has arranged the material in three parts: Part 1 (8 chapters) deals with the animal organism—important problems and characteristics of living matter, protoplasm and its properties, theories of the origin of living matter, the structure, function and types of cell, reproduction, and classification of animals. Part 2 (17 chapters) is concerned with types of animals. In Part 3 (8 chapters) the development, adaptation, and relation of animals are discussed.

While the subject matter leads from the simpler to the more complex forms, provision has been made for those teachers who prefer to introduce the student first to representatives of one group and from that viewpoint approach the lower or higher animals. The volume is profusely illustrated, many of the figures having been especially prepared for the text. A bibliography of 8 pages, a glossary of 37 pages, and a detailed index conclude the volume.



PRINCIPLES OF ANIMAL BIOLOGY. *Fifth Edition.*

By A. Franklin Shull, with the Collaboration of George R. Larue and Alexander G. Ruthven. McGraw-Hill Book Company, New York and London. \$3.50. 9 x 5½; xiv + 417; 1941.

The present revision of this standard text (cf. Q. R. B., Vol. 5, No. 2; Vol. 9, No. 4 for mention of the 3rd and 4th editions) maintains the high degree of workmanship characteristic of the earlier editions. The most important changes to be noted are those relating to physiology. The rapid advance of knowledge in this field has required that substantial changes be made in the text with regard to the composition of the blood, the chemistry of muscular contraction, and the physiology of nerve impulses. The newer trends of biological pedagogy, i.e. emphasis on the study of function rather than structure of the living

organism, and the presentation of the individual as an integrated whole rather than a group of parts, have been carefully interwoven into the textual material. In contrast to the long list of standard texts which are organized around "type" organisms, the present one is developed along the broad lines of biological principles, concepts, and theories.

The text is profusely illustrated, and each chapter carries a list of references for supplementary reading. Present also are a 36-page glossary and a complete index.



ELECTRIC EEL CALLING. *A Record of an Artist's Association with a Scientific Expedition to Study the Electric Eel at Santa Maria de Belém do Pará, Brazil.*

By Shelby Shackelford. Charles Scribner's Sons, New York. \$3.00. 9 x 6½; x + 258; 1941.

Mrs. Shackelford makes a live and colorful book out of the trip to the Amazon in search of the electric eel. While her husband, the physicist, and his associate, the biologist, explored this biological phenomenon, she, the artist, painted the ancient city of Pará and its inhabitants not only figuratively but also literally.

The daily life of the investigators is dramatized through the eyes of an artist and philosopher, and is well portrayed not only in words but also by drawings which are original and well executed. However, this is not solely a novel, for the account of the researches on the electric eel are accurately described with the result that much material previously published only in technical journals is now made available to the general reader. Aside from the electric eel, the book is filled with tales of the local color of the Brazilian city, its environs, and the daily life of its people. This is indeed a fine book to read for both pleasure and profit.



BIOLOGY OF THE LABORATORY MOUSE.

By the Staff of the Roscoe B. Jackson Memorial Laboratory. Edited by George D. Snell. *With a Chapter on Infectious Diseases of Mice*, by J. H. Dingle. The

Blakiston Company, Philadelphia. \$7.00. 9 x 5½; ix + 497; 1941.

An important volume for the experimentalist. The authors have gathered together the widely scattered literature on the mouse as a laboratory animal, filling in important gaps by special research projects. The book is designed especially as a reference work. Dealing only with the mouse it

presents a vertical cross-section of biological knowledge rather than the more usual horizontal cross-section. It contains information about one animal drawn from various branches of zoology, rather than information about one branch of zoology drawn from observation of a variety of animals.

The chapter headings are as follows:

The early embryology of the mouse; Reproduction; Histology; Spontaneous neoplasms in mice; Gene and chromosome mutations; The genetics of spontaneous tumor formation; The genetics of tumor transplantation; Endocrine secretion and tumor formation; The milk influence in tumor formation; Inbred and hybrid animals and their value in research; Parasites; Infectious diseases of mice; Care and recording.

Numerous tables and 170 figures accompany the text, and the work concludes with a bibliography of 341 titles and a detailed index.



FLEAS OF EASTERN UNITED STATES.

By Irving Fox. Iowa State College Press, Ames, Iowa. \$3.00. 8½ x 5½; vii + 191; 1941.

The medical importance of fleas in the transmission of disease is becoming increasingly recognized. The writer points out that no key to fleas has appeared since Baker's monumental work on *Siphonaptera* was published in 1904. The purpose of this work is to bring up to date the knowledge of fleas inhabiting the region east of the one-hundredth meridian, with the exclusion of Texas. Fifty-five species, falling into five families comprising thirty-three genera, occur in this area. They parasitize seventy-five mammalian and avian hosts according to our present knowledge. The fact that man and domestic animals fall within this sphere adds to the importance of the present publication.

The synonymic and host indices ap-

pended add to the value of the text. The work contains a selected bibliography and an index. Following the index are 166 excellent figures arranged on 31 plates.



A REVISION OF THE NEARCTIC HEMEROBIIDAE, BEROETHIDAE, SISYRIDAE, POLYSTOCHOTIDAE AND DILARIDAE (NEUROPTERA). *Proceedings of the American Academy of Arts and Sciences, Volume 74, Number 7.*

By F. M. Carpenter. *American Academy of Arts and Sciences, Boston.* \$2.25. 10 x 7 $\frac{3}{8}$; 88; 1940 (paper).

After examining something over 8,000 specimens of the five families of insects mentioned, the author has compiled this revision, which includes 14 genera and 66 species of Neuroptera. One genus and 17 species are described as new. In addition to the detailed keys to each family, the text includes such additional taxonomic information as distribution, habitat, natural history, and descriptions of the genitalia and wing venations of the various species.

A bibliography of 98 titles, a series of plates illustrating wing venations, and an index to families, genera, and species conclude the monograph.



ATLAS OF THE SCALE INSECTS OF NORTH AMERICA. *Series III, 269-384.*

By G. F. Ferris. *Stanford University Press, Stanford University, Calif.; Oxford University Press, London.* \$7.75 (cloth); \$6.75 (paper). 10 $\frac{1}{4}$ x 9; [236 unnumbered] + 116 plates; 1941.

This volume, the third of a series (cf. Q.R.B., Vol. 13, p. 360 for notice of the first) which is being prepared with the ambitious aim of describing every species of scale insect in North America, is devoted to 59 members of the Tribe Diaspidini and 57 of the Tribe Aspidiotini, both belonging to the Family Diaspididae. The excellent plates are the main feature of the book. A minimum of textual matter gives information on the distribution, hosts, habits, recognition characters and miscellaneous items to aid in the

identification. The series is of primary interest to economic entomologists.



BIRD ISLANDS DOWN EAST.

By Helen G. Cruickshank. *The Macmillan Co., New York.* \$2.50. 8 $\frac{3}{8}$ x 5 $\frac{1}{2}$; xii + 123; 1941.

The wife of a well-known ornithologist herein recounts the adventures with her husband among the offshore islands of Maine. To reach these islands is quite an undertaking in itself, and the struggles these bird students had against the waves and the fog give a salty marine flavor to the narratives. Naturally only sea birds are discussed, among these being puffins, petrels, gulls, guillemots, cormorants, terns, and phalaropes. The colonial life of the birds is well related and considerable information is given concerning the natural history of these small and practically inaccessible islands. Some of Mr. Cruickshank's most interesting photographs illustrate the book.



BOTANY

AMOS EATON. *Scientist and Educator 1776-1842.*

By Ethel M. McAllister. *University of Pennsylvania Press, Philadelphia; Oxford University Press, London.* \$5.00. 9 x 6; xiii + 587; 1941.

"NOBLE FELLOW" William Starling Sullivant. *With a Compilation of the New Species of Mosses and Liverworts Described by William S. Sullivant and Those Described by William S. Sullivant and Leo Lesquereux, Prepared by Richard T. Wareham.*

By Andrew D. Rodgers III. *With a Foreword by Adolph E. Waller. G. P. Putnam's Sons, New York.* \$3.50. 8 $\frac{3}{8}$ x 5 $\frac{1}{2}$; xxii + 361; 1940.

These are well-written biographies of two leading botanists of the early 19th century who are not as well remembered by posterity as they should be. Although both of these men seem to have been on very intimate terms with John Torrey and Asa Gray, there is no evidence that they ever met. Sullivant was a specialist in the

narrow field of biology, but Eaton was a zoologist, a mineralogist, and a geologist as well as a botanist.

MacAllister treats the different phases of Eaton's activity separately, but this does not mean that Eaton took these studies by turns. All his life he was devoted to all branches of natural history, and although it is on account of his researches in systematic botany that he is chiefly remembered today, on one occasion he disavowed being a botanist.

He was a New Yorker by birth and descent, his ancestors having been among the original Dutch settlers of New Amsterdam, and it was in that state that most of his work was accomplished. The crowning achievement of his career was the establishment and development of the Rensselaer Institute in Troy, on whose faculty he taught for many years.

Sullivant, on the other hand, was a westerner. He was born in Ohio, when that was a western state, and his ancestors had been pioneers there for many generations. The first chapter of his biography is devoted to his genealogy. While exploring in the Northwest Territory he corresponded with all the leading naturalists of England and France, and the position which he finally achieved in the botanical world is indicated by the fact that the leading international bryological society bears his name—The Sullivant Moss Society.

Both books are well illustrated and indexed and have extensive bibliographies.



THE PLANT DOCTOR. *The How, Why and When of Disease and Insect Control in Your Garden. Revised Edition, with New Chapters on Regional Plant Troubles.*

By Cynthia Westcott. Frederick A. Stokes Co., New York. \$2.00. 7½ x 4½; xx + 297; 1940.

This book is entirely different from any other garden book and should be in the possession of everyone interested in gardening. In a simple, yet entertaining style the author verbally takes the reader into the garden and, week by week, discusses and describes the insect pests and plant diseases that are apt to occur at that

time, and the most effective methods of preventing and controlling them. Numerous black and white drawings illustrate and simplify the text.

After publishing the first edition of *The Plant Doctor*, the author spent four years traveling and studying plant pests and diseases in other parts of the country as well as in the Eastern States. Her observations are included in this revised edition. There is also a chapter on house plants, a condensed alphabetical miscellany, and a list of books recommended for additional reading.



TREE-RING ANALYSIS AND DATING IN THE MISSISSIPPI DRAINAGE. *With Appended Papers: Reflection of Precipitation and Temperature in Tree Growth*, by Mildred M. Wedel and Florence Hawley; *A New Dendrochronograph*, by E. J. Workman and Florence Hawley.

By Florence Hawley. Chicago University Press, Chicago. \$1.50. 9½ x 6½; xi + 110 + 8 plates; 1941 (paper).

An introductory chapter describes the instruments and techniques employed in tree-ring work and an account of previous work in the Mississippi drainage. Then follows a detailed description of four seasons' work in analyzing tree rings of living trees, old logs and beams in order to obtain information on floods and droughts in the past, and of semi-decayed wood and charcoal from old Indian mounds and ruins to estimate their age.

A special technique for the preservation of mound specimens, especially charcoal, was developed for use by archaeologists and it is expected that certain dating of these specimens is possible and should be accomplished in the near future.



HILFSBUCH FÜR DAS SAMMELN UND PRÄPARIEREN DER NIEDEREN KRYPTOGAMEN. *Zweite neubearbeitete Auflage.*

By Gustav Lindau. *Zweite Auflage* by O. C. Schmidt. Gebrüder Borntraeger, Berlin. RM. 3.60. 7½ x 4½; vii + 93; 1938.

This pocket-size handbook contains gen-

eral directions for collecting, preserving and labelling specimens of cryptograms, and specific methods for the various species of fresh-water and salt-water algae, myxomycetes, fungi, lichens and mosses. Bacteria and the colorless flagellata, which cannot be studied by *Rucksack* methods, are omitted. Changes from the first edition include the incorporation of more recently perfected methods, the expansion of data on occurrence, and the addition of a bibliography. There is a subject index.



THE ANAEROBIC BACTERIA AND THEIR ACTIVITIES IN NATURE AND DISEASE. *A Subject Bibliography. Supplement One, Literature for 1938 and 1939.*

By L. S. McClung and Elizabeth McCoy. University of California Press, Berkeley. \$3.50. 11 x 8; xxiv + 244; 1941.

Except for the creation of a section to cover the prophylactic use of toxoid in immunization and the citation of the complete title of each reference, this first supplement follows the general plan of the original volume (cf. Q.R.B., Vol. 15, p. 98). In addition to the literature for 1938 and 1939 some titles for 1940 have been included. A useful reference work. It is to be hoped that the authors will prepare further supplements.



PLANT ECOLOGY. *Third Edition, Thoroughly Revised.*

By W. B. McDougall. Lea and Febiger, Philadelphia. \$3.00. 9½ x 5½; 285; 1941. This edition of an excellent text (cf. Q.R.B., Vol. 3, p. 141; Vol. 4, p. 366) follows the same general order of presentation as the earlier texts, with considerable space, as formerly, being given to a discussion of symbiotic phenomena. The many excellent figures form an important part of the text.



TROPICAL AMERICAN FERNS. University of California Publications in Botany, Volume 19, No. 9.

By Edwin B. Copeland. University of California Press, Berkeley and Los Angeles. \$1.00. 10½ x 6½; 23 + 31 plates; 1941 (paper).

In addition to the descriptions of the ferns included in this list are interesting notes by the author discussing generic differences, distribution, etc. The fine photographic plates (31 in number) are, with three exceptions, illustrations of types.



MORPHOLOGY

PATTERNS AND PROBLEMS OF DEVELOPMENT.

By C. M. Child. University of Chicago Press, Chicago. \$8.00. 9½ x 6½; ix + 811; 1941.

It is always pleasant to welcome a book based on a life-time of research that summarizes a field and collates loose ends. Such a book is Child's *Patterns and Problems of Development*. The axial gradient theory has been the subject of much debate among biologists for at least 40 years. Today, there are few workers who deny the existence of such gradients in many organisms. However, there are students, particularly the experimental embryologists, who view these metabolic gradients as mere expressions of some deep-seated activity and not as factors that regulate the *pattern* of growth and differentiation. Briefly put, the issue seems to be this: Can quantitative or rate factors, such as the gradients, initiate differentiation in a specific protoplasmic substrate, or, are there particular chemical substances or qualities produced within the organism that organize the protoplasm during early development with the gradients simply emerging as by-products of this organization? Child, of course, inclines to the former view and many embryologists to the latter. The problem is not yet settled. There are data that support both contentions. Be that as it may, Child advances in this book some cogent points in favor of his position. Also, his material has the virtues of good documentation with many examples and a point of view that is broad. The author conceives of development as something more than

the embryologic period. On this issue he says:

Developmental physiology is often regarded as if it were concerned only with embryonic development, and for some authors of recent years it seems to be very largely a matter of vertebrate or even of amphibian development. It cannot detract in any way from the great interest and importance of the experimental work of Spemann, his students, and many others on amphibian development to point out that this and development of vertebrates generally constitute only a small part and, so far as fundamental problems are concerned, probably not the most important part of the field of developmental physiology. . . . There are many other forms of development, with other starting-points than eggs. Some of them, such as buds, reconstitutions of isolated pieces, and development of cell aggregates, bring us much nearer the beginnings of developmental patterns and the factors concerned in their origins and permit more extensive control and analysis than do most eggs and embryos. In fact, embryonic development appears generally to be the most highly specialized form of development. (page v.)

The book is organized somewhat as follows: first, the problem is delineated and the nature of gradients and the experiments that demonstrate them are discussed, using a wide range of material; second, the gradient theory is applied to a series of developmental problems, e.g., the "organizer" concept, cleavage, and the initiation of embryonic pattern; finally, the material is discussed generally in a chapter on physiological integration where the gradients are related to development somewhat in the causal fashion indicated above.

The book is admirably bound and documented. There are a number of fine drawings, an excellent bibliography and index, and a series of appendices concerned largely with methods.

This is an excellent comprehensive synthesis of the axial gradient problem and its implications and applications. It leaves certain points unsettled as the author readily recognizes and unquestionably there are statements with which certain biologists will disagree. But it is a tribute to the life work and ideas of a distinguished American scholar in the field of biological science.



DAS LABYRINTH. Bau, Funktionen und Krankheiten des Innenohrs vom Standpunkte

einer experimentellen und vergleichenden Pathologie.

By Cl. F. Werner. Georg Thieme Verlag, Leipzig. RM. 28.50 (cloth); RM. 27.00 (paper) (outside of Germany). 9½ x 6½; xvi + 400; 1940.

Probably no other organ of the body requires such specialized techniques of study as does the inner ear; so that, notwithstanding the importance of the ear for both hearing and equilibrium, investigations on the subject are today as before the prerogatives of only a few. Apparently aware of this the author has brought together the scattered information about the labyrinth in order to present an adequate summary of the recent and the established methods of investigation and the new discoveries about the function and the structure of this organ. Although sufficient mention is made of the diseases of the inner ear in man, emphasis is placed on the experimental approach to the study of the normal and pathological reactions of the cochlear and vestibular apparatus. In order, the author outlines first the techniques employed to examine clinically and experimentally the functional status of the ear. He then describes briefly the anatomy and histology, giving particular attention to the histological preparations. The chapters that follow describe fully the physiology of the labyrinth from observations and from experimental procedures. Among the latter, first place is given, of course, to the experiments based on the discovery of action currents. In the final chapters the effects of vitamins, of hormones, and of tumors are discussed.

The presentation is sound, detailed, and clear, and a very good list of references accompanies the text.



A LABORATORY GUIDE TO THE STUDY OF DEVELOPMENTAL ANATOMY.

By A. Byron Leonard. Burgess Publishing Co., Minneapolis, Minn. \$1.50. 10½ x 8½; iii + 75; 1941 (paper).

This outline is intended to serve as an adequate guide for the student in a laboratory course in pre-medical embryology. The author, realizing that although draw-

ings frequently made by the student often require more time than the results justify, but believing that these student drawings frequently enable him to observe relations that might otherwise be missed, has here attempted a compromise—drawings have been reduced in number and in detail, while preserving the advantage of careful student observation. After suitable study of mitosis, meiosis, fertilization, spermatogenesis and oogenesis, the outline proceeds to elaborate and concentrate on the various stages of the chick and ten-millimeter pig embryos. The series of plates, containing 142 carefully and completely labelled drawings, are especially commendable and constitute an important feature of the outline. The author has kept constantly before the student the concept that the developing organism is a discreet individual, with its own environmental problems presented for solution, even as the fully-developed organism has its problems of adjustment to environment. Space is provided for drawings and for lecture notes. Suggested reading references are placed at advantageous points in the book. There is no index.



TEXT-BOOK OF COMPARATIVE HISTOLOGY.
By Elbert C. Cole. The Blakiston Co., Philadelphia. \$4.00. 9 x 5½; vii + 396; 1941.

In this completely authoritative and excellently prepared work, Cole has not only presented the subject from the logical, though somewhat neglected, comparative point of view, but has gone a step further to include the invertebrates as well in his pertinent discussion.

The textual material has been built up in four parts; namely, (1) a brief introductory section dealing with the history of the subject, the nature of the cell, the mechanics of cell division, and the origin of the various types of cells and tissues in the developing embryo; (2) a detailed study of the structure and function of the six fundamental types of cells; (3) a lengthy consideration of the body organs and organ systems as tissue complexes; and (4) a final short section on the care and use of instruments essential to the

study of histology, and a list of accepted procedures in histological technique.

The volume is profusely illustrated, and each of the 22 chapters is supplied with a well-selected list of references. The complete index adds to its value for classroom or reference use.



COMPARATIVE CHORDATE ANATOMY. A Laboratory Text.

By Clair A. Hannum. Stanford University Press, Stanford University, California. \$2.00. 8½ x 5½; vii + 211; 1941.

This volume is designed for those courses of anatomy in which the empirical observations of the laboratory are subordinated to the broad generalizations that may be drawn from an assemblage of such observations. The present text follows the "type study" method of presentation, in which a variable number of representative chordates are utilized to illustrate the evolutionary processes that have culminated in the modern vertebrate. After suitable introductory material on the chordates, phyletic origins and ontogenesis, the following vertebrates are studied: balanoglossus, a simple ascidian, amphioxus, the fresh water lamprey, the shark, necturus, the turtle, the pigeon, and the rat. The book is very carefully and completely indexed, but contains no illustrations or list of references. This laboratory text should be well received by those teachers using the "type study" method of instruction in comparative anatomy.



A LABORATORY MANUAL FOR HISTOLOGY.

By James Forbes. Fordham University Press, New York. \$1.25. 9½ x 5½; vi + 74; 1941 (paper).

After proving its worth in the elementary histology course at Fordham University, this little manual is now ready for wider distribution and use. The work outlined is not intended to take the place of a textbook, but rather, to supplement any good text in the laboratory phase of the course. In addition to the required draw-

ings for each laboratory exercise, there are lists of questions designed to bring out the fundamental relationships between microscopic and gross structure, between structure and function, and between structure and development. The volume carries a short table of contents, and a list of references.



PHYSIOLOGY AND PATHOLOGY

NATURAL RESISTANCE AND CLINICAL MEDICINE.

By David Perla and Jessie Marmorston. Little, Brown and Company, Boston.

\$10.00. 9½ x 6½; xx + 1344; 1941.

This monumental work leaves few pathways unexplored that lead toward an understanding of natural resistance to infectious diseases. It is a survey of the biology of natural resistance in health and disease and an analysis of the various factors that have a part in determining or modifying these conditions.

It was not many years ago that variations in resistance seemed to hinge on the virulence of the infecting micro-organisms, although individual variations seemed, possibly, attributable to "constitution." More recently it has been recognized that "such 'constitutional' differences while in part dependent upon genetic factors are to some degree expressions of the functional activity of the glands of internal secretion and that such variations definitely influence the course of infections." The possibility that the thyroid, thymus, the suprarenal and the sex glands, the spleen, the lymph glands, and the microphage tissue may all have some part in both natural and acquired resistance is now recognized.

The difference between natural and acquired resistance is clearly stated by the authors: "While acquired immunity depends upon the presence of antibodies and on an altered state of the tissues in their reaction to reinfection, natural resistance is dependent upon a different fundamental mechanism, modified by a great variety of biological factors."

The ten sections in the volume treat resistance from the following angles:

heredity; age; sex; other endocrine glands; humoral and cellular mechanisms; liver, body surfaces and nervous system; diet; certain depression states; climate; and clinical aspects. Each of these sections has been summarized and concludes with a list of references, the total number of these titles running to something over 5,000. While recognizing the importance of the psychological and mental factors in resistance, the authors do not enter this field because "the evidence does not lend itself to critical analysis." Also the socio-economic factors, being outside of a biological treatise, have not been discussed, although the very great importance of this aspect is recognized.

A carefully prepared index concludes this useful survey.



THE STORY OF CLINICAL PULMONARY TUBERCULOSIS.

By Lawrason Brown. The Williams & Wilkins Company, Baltimore. \$2.75. 8½ x 5½; ix + 411; 1941

This book, which embodies the lectures that Lawrason Brown delivered to his students, outlines the changes in the diagnosis and therapeutics of phthisis from the time of Hippocrates to the modern days of artificial pneumothorax. In the classical manner, Brown divides the historical sequence into four periods: the first ranges from ancient times up to the middle of the 17th century; the second continues on to the beginning of the 19th century; the third, to the latter part of that century; and the fourth, from Koch's discovery to the present. The knowledge and practices of each period are epitomized in an interesting fashion by an integrated description of the clinical procedures which were followed by the eminent physicians of the period. The figure of Laennec assumes gigantic proportions in this account as his contributions are re-stated time and time again. Brown had apparently a tremendous admiration for the French physicians and dwells at great length on their work. There are, however, also chapters on the progress manifested in this country, England, Germany, and Austria, and on the development of

artificial pneumothorax. To round out the subject, special chapters on the writings of Laennec, on the stethoscope, and on early medical journals are included. In addition, Sampson contributes a chapter on the diagnostic use of the x-ray in pulmonary tuberculosis, and Archibald discusses surgical treatment. Both of these chapters, as well as the previous sections, represent well-written, authoritative surveys of the subject, but the work, because of its fragmentary nature, cannot be regarded as history in the technical sense. It will, however, furnish the medical historian as well as the lay reader the means to evaluate the significance of the changes in the clinical handling of pulmonary tuberculosis.



A TEXTBOOK OF DIETETICS.

By L. S. P. Davidson and Ian A. Anderson. *With Diet Sheets Constructed by Mary E. Thomson. Foreword by Sir John B. Orr. Paul B. Hoeber, Inc. (Medical Department of Harper and Bros.), New York.* \$4.25. 8½ x 5½; xviii + 324; 1941.

The field of dietetics is at least one in which the general practitioner can carry out his double rôle of service in promoting health and curing disease. Up to the present time, however, it has been difficult for him not only to keep pace with the advance of knowledge in nutrition, but also to translate the results of animal experimentation into terms of human health and disease. In the face of these facts there has been a real need for a book which would present the latest knowledge of nutrition in such a form as to be of immediate and practical use to the practicing physician. The present volume has grown out of an abundance of experience in the dietary treatment of human ills, as well as from experimental work on animals, on the problem of nutrition.

The work covers such wide topics as the physiology of nutrition, diet in periods of physiological stress, and dietetic treatment in established diseases. Throughout the volume there is a plea for closer cooperation between the laboratory research worker and the general prac-

titioner in the hope that the time lag between laboratory experimentation and practical application will be cut to a minimum. The volume is further enhanced by a group of tables, recipes, and diet sheets to be used by the physician in making his dietary recommendations in various diseases that are directly or indirectly affected by the nutritional state of the patient. The list of selected references and the complete index also contribute to the value of the book for the overworked general practitioner.



ENDOCRINOLOGY. *The Glands and Their Functions.*

By R. G. Hoskins. W. W. Norton and Company, New York. \$4.00. 8½ x 5½; 388; 1941.

The importance of the delicate balance of the endocrine system in relation to man's physical and mental well-being is reason enough for the present intense interest, and rapid advance, in the field of endocrinology. The extensive and diversified clinical and laboratory experiences of Hoskins, in relation to the glands and their functions, have well qualified him for the task of preparing this comprehensive volume. In it he has attempted to bring together in a simple and understandable form, all the pertinent knowledge concerning the endocrines in health and disease. He has wisely departed from the general text-book mode of discussing the hormones from the standpoint of animal experimentation, and has developed the subject around human case histories. Throughout his discussions, the author points out that there still exist wide gaps in our knowledge of endocrinology, and indicates the lines along which further investigation is most urgently needed, and is likely to produce the most valuable results.

The text is well supplied with illustrative material, and documentary records. The closing list of endocrine literature and the detailed index add to the volume's value for biologists, psychologists, and pre-medical students.

MUST WE GROW OLD?

By Barclay Newman. G. P. Putnam's Sons, New York. \$2.50. 8 x 5½; 269; 1941.

Another book for the layman giving a cheerful panoramic view of what research in the biological fields is doing toward the preservation and extension of human life. In Chapter I, The science of death comes to life, we read that "To man it has been given that he is master of his doom." In the next chapter, Our newest medical speciality—geriatrics [pathology of old age], the author discusses the increase in the average duration of life and the condition of the various organs in the aged. Geriatrists can be said "to be supplying the final proof that old age is pathological. . . ." In Chapter III, Death—always an accident?, we find that "Life spans are decided by chance, i.e., by (chemical) factors largely, but not entirely unknown." Then follows the longest section of the book (93 pages) on the effect that food factors have on the length of life. In this we gather that ultimately, by appropriate modification of food intake, the life of the individual can be extended indefinitely. The remaining chapters dealing with hormones, cancer, hypertension, tissue culture, enzymes, genes, etc., all present the same happy picture for the future of the human race. On almost every page the writer mentions the research work of well-known biologists, but he gives no reference lists nor does he furnish an index.



HEALTH OF WHITE SETTLERS IN SURINAM.
Colonial Institute at Amsterdam Special Publication No. LIIII. Department of Tropical Hygiene No. 16.

By N. H. Swellengrebel, in collaboration with E. van der Kuyp. *Colonial Institute at Amsterdam.* Fl. 2, 10. 8½ x 6½; viii + 118; 1940 (paper).

This report is not intended so much to encourage white colonization of Dutch Guiana as it is to evaluate the public health of the white settlers of the past and present. Although tropical disease is credited with some measure of the failures of the white colonies of the past,

the present author believes that the big problem for future settlers will be economic rather than medical. With a reasonable amount of sanitary precaution, the coastal region and various parts of the inland regions of Surinam appear to be conducive to European settlement, that is, provided the Europeans, in their struggle for a livelihood, do not have to compete with Asiatic labor and Asiatic standards of living. The strongest recommendation listed, with regard to health, is that future white settlers be rigidly segregated from the native colored population in respect to living quarters, schools, and daily activities. The study is indicative of the enormous amount of research and field work that has been done in surveying the public health conditions of Surinam. It is well documented and indexed.



DAS MENSCHLICHE KNOCHENMARK: Seine Anatomie, Physiologie und Pathologie nach Ergebnissen der intravitalen Sternalpunktion.

By Karl Robr. Georg Thieme Verlag, Leipzig. RM. 29.25 (cloth); RM. 27.75 (paper) (outside of Germany). 9½ x 6½; 286; 1940.

Over 1800 sternal punctures, made over the course of seven years, are the main basis of this study of bone marrow as a blood-forming organ. The author divides the book into two parts. The first, or general, section gives a review of studies and theories concerning the embryological, anatomical, cytological, physiological and pathological aspects of the subject, and the development of the sternal puncture method for use in the study of bone marrow in the living subject. The second, or specialized, part presents the results of the author's investigations on erythropoiesis, leukopoiesis and thrombopoiesis under normal conditions and in the presence of leukemia, aplastic anemia, tumors of the bone marrow and infectious diseases. The 125 illustrations (some of them in color), which deserve special mention, add greatly to this valuable contribution to the literature of bone marrow and its functions.

BIOLOGICAL SYMPOSIA, *Volume III. Muscle.*
Series Edited by Jacques Cattell. Volume
III Edited by Wallace O. Fenn. Jacques
Cattell Press, Lancaster, Pennsylvania.
 \$3.50. 9½ x 6½; 370; 1941.

This volume, containing 15 articles by various authors on muscle physiology, grew out of the symposium on muscle which took place at the American Physiological Society meetings at New Orleans in April, 1940. With the four papers originally presented—Muscle function as studied in single muscle fibers, by Robert W. Ramsey and Sibyl F. Street; Action potentials and conduction of excitation in muscle, by Emil Bozler; The regulation of energy exchange in contracting muscle, by Dugald E. S. Brown; and Changes during muscle contraction as related to the crystalline pattern, by Ernst Fischer—several other articles on closely related aspects have been grouped. The scope of interest of the volume has been expanded and rounded out by the inclusion of several contributions on muscle chemistry and myoneural transmission, grouped together at the end. Fenn has provided an introduction in which the history of muscle investigations and indications for future work are presented.



YOUR TEETH: Their Past, Present, and Probable Future.

By Peter J. Brekhus. With a Foreword by Irvine McQuarrie. University of Minnesota Press, Minneapolis. \$2.50. 8 x 5; xvii + 255; 1941.

According to the writer of this treatise nearly all of our dental ailments, caries, pyorrhea, malocclusions, and to a certain extent anomalies, have one underlying cause—civilization. This theme is presented 255 + xvii times. Although the repetition becomes tiresome the belief is not without some justification, as Brekhus shows by evidence from racial and nutritional studies. He further discusses the history of dentistry, delves into the comparative anatomy and evolution of dental structure, describes the relation of oral to general health, and seeks for the evasive causes of caries and pyorrhea. The conclusion is drawn that at present our only

hope is to inaugurate an inexpensive and all-inclusive plan of regular dental treatment for America's children. Hope for the future must center in increased dental research founded on the biological and physical sciences. *Your Teeth* is interestingly and amusingly written, and at the same time is based on numerous authoritative references.



ANNUAL REVIEW OF PHYSIOLOGY. *Volume III.*

Edited by James M. Luck and Victor E. Hall. Annual Reviews, Inc., Stanford University, P. O., Calif. \$5.00. 8½ x 5½; viii + 784; 1941.

This indispensable *Annual* has temporarily lost its international character. This, however, is inevitable, since, in the first place, many European physiologists, for a number of reasons, have been unable to collaborate, and in the second, foreign periodicals have circulated most irregularly. In this country some of the contributors have entered war service and have been unable to prepare assigned articles. Nevertheless, we find this volume, with its 26 sections, a valuable addition to our reference books. Among the topics discussed we note: Energy metabolism, Respiration, Muscle, Blood, Peripheral circulation, and Endocrine aspects of the physiology of reproduction. Sweden is represented by a group of three articles on the special senses (hearing, visual receptors, and vibratory sensations and pain); England, by a section on histamine and anaphylaxis. As usual the volume has an author index and a detailed subject index.



SCIENCE AND SEIZURES. *New Light on Epilepsy and Migraine.*

By William G. Lennox. Harper and Brothers, New York and London. \$2.00. 8 x 5½; xiii + 258; 1941.

In the introductory chapter Lennox states the reasons for his book: first, as an aid to physicians who require in concise form the most recent information on epileptic and

migraine attacks; second, to help the patient to maintain a rational attitude toward his ailment and to cooperate with the physician; and third, to dispel the ignorance and prejudice of the general public. In large measure the book has achieved its purpose, although it leaves one with the knowledge that the surface has hardly been scratched in our attack on epilepsy. The latest scientific studies of cause, diagnosis, prevention, and treatment are recorded in these pages. This includes X-ray, electroencephalography, psychoanalytic treatment, and the use of drugs. In addition such sociological factors as education, occupation, and marriage are given due consideration. Lennox closes with a call for increased research in several fields which offer promise of success in the understanding and treatment of seizures.



AMERICA ORGANIZES MEDICINE.

By Michael M. Davis. Harper and Brothers, New York and London. \$3.00. 8½ x 5½; viii + 335; 1941.

With increasing specialization of medical science there has occurred a marked change in patient-doctor relationships and a rising cost of medical services. Altered socioeconomic conditions have made for increased disparity of treatment among various classes. Davis discusses these trends and the measures which have been used in coping with the problem, including public health centers, welfare services, clinics, health legislation and medical insurance plans, to mention a few. The efficacy of each of these actions and agencies is frankly criticized, pro and con. No definite program is put forward as a solution to the problem, but the author hopes that his book may diminish partisanship among the various agencies and further a form of organization which will promise adequate treatment for all people, at the same time maintaining individuality and freedom of choice for doctors and patients alike. This volume is thoroughly indexed and contains a bibliography of nineteen pages.

THE WORK OF THE KIDNEYS. *A Guide for Use with the Instructional Sound Film "The Work of the Kidneys."*

By Melvin Brodshaug and Helen Haggerty, in Collaboration with A. J. Carlson, H. G. Swann and F. J. Mullin. University of Chicago Press, Chicago. 15 cents. 7½ x 5½; iv + 26; 1941 (paper).

CONTROL OF BODY TEMPERATURE. *A Guide for Use with the Instructional Sound Film "Control of Body Temperature."*

By Melvin Brodshaug and Helen Haggerty, in Collaboration with A. J. Carlson, F. J. Mullin and H. G. Swann. University of Chicago Press, Chicago. 15 cents. 7½ x 5½; iv + 25; 1941 (paper).

Both of these guides have been prepared as aids in making the most effective use of the sound films on these subjects which were prepared, in collaboration with the authors, from materials in introductory general courses in the biological sciences. High-school teachers and college instructors will find both the films and the guides useful as additional material in classroom work.



PEDIATRIC BIBLIOGRAPHY. *Monographs of the Society for Research in Child Development, Volume VI, No. 1 (Serial No. 27).*

By A. Graeme Mitchell. Society for Research in Child Development, National Research Council, Washington, D. C. 75 cents. 9 x 5½; vii + 119; 1941 (paper).

This 120-page bibliography was originally designed to be included in the third edition of *A Textbook of Pediatrics* (J. P. Crozen Griffith and A. Graeme Mitchell). Since it was found impractical to publish it there, it has been published separately. The list includes both textbooks and original articles from leading scientific journals, and is organized around the chapter headings of the above-mentioned volume, namely: the diseases of the various organs and organ systems, and diseases attributed to pathogenic organisms.

The work will be of value not only to students using the Griffith-Mitchell textbook, but to the general practitioner and the specialist in pediatrics.

THE BACTERIOLOGY OF PUBLIC HEALTH.

By George M. Cameron. C. V. Mosby Co., St. Louis. \$3.50. 8½ x 5½; 451; 1940. Instead of accepting the dictum that a little knowledge is dangerous the author takes the position that some knowledge, however limited, can at times be helpful. He believes that in the case of parasitic diseases particularly, an understanding of the life and activity of the microorganism will be valuable to the layman. He, therefore, reviews briefly all the diseases caused by protozoa, bacteria, fungi, or viruses, and for each outlines the life cycle of the parasite, the mode of infection, the diagnostic tests, and specific therapy, if any. Well-selected references are given so that the interested persons can pursue the inquiry further. As a college textbook for supplementary reading in hygiene this volume will be found very useful.



PUBLIC HEALTH AND HYGIENE. A Students' Manual. Third Edition.

By Charles F. Bolduan and Nils W. Bolduan. W. B. Saunders Company, Philadelphia and London. \$3.00. 7½ x 5½; x + 366; 1941.

Students of medicine, nursing, and public health will find this book valuable because of the large amount of substantial material it contains. The subjects presented are not only fairly complete but are also up to date. Thus the volume will also serve as a good review book for examinations. The wealth of material present can best be shown by a brief listing of some of the chapters. These are as follows: Life history of certain important insects, Principles of nutrition, Disinfection, Food poisoning, Dysentery and cholera, Our changing health problems, Diseases of later life, Food inspection, Public health nursing, Epidemiology and public health, Vital statistics. The material is well indexed but there is no bibliography.



NOTES ON DIFFUSE SCLEROSIS, DIFFUSE GLIOMATOSIS AND DIFFUSE GLIOBLASTOMA-

TOSIS OF THE BRAIN WITH A REPORT OF TWO CASES. *Acta Jutlandica Aarsskrift for Aarhus Universitet XII*, 3.

By Lårus Einarson and Axel V. Neel. Einar Munksgaard, Copenhagen. Dan. Cr. 2.50. 9½ x 6½; 56; 1940 (paper).

The authors discuss their classification of demyelinating and sclerotic processes in the brain which they have presented in a previous work (1938) and report two further cases which they believe are pertinent to the question of the existence of a glioblastomatous transition form of diffuse sclerosis in the anatomical sense of the word. The clinical histories, autopsy findings and histological examinations of the brains of both cases are reported in detail. The pathogenesis of these diffuse blastomatous reactive growths and of diffuse glioblastomas is discussed and the possibility of transition forms considered. A list of references is included.



PERSON UND CHARAKTER.

By Rudolf Thieme. Georg Thieme Verlag, Leipzig. RM. 1.50. 8½ x 5½; 43; 1940 (paper).

This is a brief discussion of the factors, mental and physical, environmental and inherited, that must be considered in the total make-up of a "personality." Characteristics thought important in aiding the typing of individuals according to constitutional or personality groups are indicated. The volume is annotated.

THE UNIVERSITY AND PUBLIC HEALTH STATESMANSHIP. *University of Pennsylvania Bicentennial Conference M-17*.

By Arthur P. Hiscbens, Harry S. Mustard, Waller S. Leathers, and Charles-Edward A. Winslow. University of Pennsylvania Press, Philadelphia. 50 cents. 9 x 6; 33; 1941 (paper).

PROBLEMS OF INTESTINAL OBSTRUCTION. *University of Pennsylvania Bicentennial Conference M-13*.

By John P. Peters, Owen H. Wengensteen, W. Osler Abbott, Allen O. Whipple and

John A. Nelson. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 56; 1941 (paper).

THE RELATION OF DISEASES IN LOWER ANIMALS TO HUMAN WELFARE. *University of Pennsylvania Bicentennial Conference, M-14.*

By John R. Mohler, Raymond A. Kelser, and Cassius Way. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 39; 1941 (paper).

MODERN ASPECTS OF THE ANTITUBERCULOSIS PROGRAM. *University of Pennsylvania Bicentennial Conference, M-15.*

By J. Burns Amberson, Kendall Emerson, Wm. Charles White, and Louis I. Dublin. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 38; 1941 (paper).

CAUSE AND GROWTH OF CANCER. *University of Pennsylvania Bicentennial Conference, M-9.*

By Louis F. Fieser, Stanley P. Reimann, Peyton Rous, Warren H. Lewis, Margaret R. Lewis, and Baldwin Lucké. *University of Pennsylvania Press, Philadelphia.* 75 cents. 9 x 6; 64; 1941 (paper).

DENTAL CARIES. *University of Pennsylvania Bicentennial Conference, M-11.*

By Henry Klein, Carroll E. Palmer, Basil G. Bibby, and Elmer V. McCollum. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 53; 1941 (paper).

MEDICAL PROBLEMS OF OLD AGE. *University of Pennsylvania Bicentennial Conference, M-4.*

By Louis I. Dublin, Howard T. Karsner, O. H. Perry Pepper, and Barney Brooks. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 46; 1941 (paper).

NUTRITION. *University of Pennsylvania Bicentennial Conference, M-5.*

By Conrad A. Elvehjem, Cyril N. H. Long, and Elmer V. McCollum. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 46; 1941 (paper).

HYPERTENSION. *University of Pennsylvania Bicentennial Conference, M-8.*

By Harry Goldblatt, Eugene M. Landis, and Alfred W. Adson. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 46; 1941 (paper).

BIOCHEMISTRY

ADVANCES IN ENZYMOLOGY and Related Subjects. Volume I.

Edited by F. F. Nord and C. H. Werkman. *Interscience Publishers, Inc., New York.*

\$5.50. 9 x 5½; x + 433; 1941.

This fine volume inaugurates a plan "to provide a medium of publication in which significant discoveries or advances, either experimental or theoretical, are presented in a more comprehensive and unified fashion than is possible in regular journals, by authors who have been closely identified with this development."

The following subjects are discussed: Protein structure, by Henry B. Bull; Physical-chemical aspects of the problem of virus activity, by Luise Holzapfel; The specificity of proteinases, by Max Bergmann and Joseph S. Fruton; Metabolic generation and utilization of phosphate bond energy, by Fritz Lipmann; The chemical nature of catalase, by James B. Sumner; Enzymes and trace substances, by D. E. Green; Photosynthesis, facts and interpretations, by J. Franck and H. Gaffron; The bacterial photosyntheses and their importance for the general problem of photosynthesis, by C. B. Van Niel; Enzymatic processes in the living plant, by A. L. Kurssanov; Digestion in the lower vertebrates, by H. J. Vonk.

Graphs and figures appear in the texts, and each chapter concludes with a lengthy bibliography. Author and subject indexes are provided.



THE AVITAMINOSSES. *The Chemical, Clinical and Pathological Aspects of the Vitamin Deficiency Diseases. Second Edition.*

By Walter H. Eddy and Gilbert Dalldorf. *Williams & Wilkins Company, Baltimore.* \$4.50. 9 x 5½; xiii + 519; 1941.

The first edition of this treatise appeared three years ago. Many changes in the present edition have been made in order to incorporate the newer knowledge in the field of avitaminoses. The volume has been enlarged by the addition of over 150 pages and a new chapter (III) has been added to furnish a clear picture of the relation of vitamins to cellular oxidation.

This discussion of vitamins from the clinical, chemical, and pathological points of view furnishes the student and the practitioner with a valuable reference work. Each chapter concludes with a list of references and there are 41 plates, 43 tables, and 28 figures in the text. In Appendix I is a discussion of the methods of studying avitaminoses, and Appendix II gives vitamin values of foods. Author and subject indexes conclude the volume.



DIE METHODEN DER FERMENTFORSCHUNG.
Lieferungen 6 and 7.

Edited by Eugen Bamann and Karl Myrbäck. Georg Thieme Verlag, Leipzig.
Lief. 6: RM. 25.20 (outside of Germany); Lief. 7: RM. 31.20 (outside of Germany). 11 x 8; Lief. 6: 1837-2172, Lief. 7: 2172-2588; 1941 (paper).

Among the many contributors to these two volumes are Kobel, Hackenthal, Nilsson, Bamann, Boyland, Holmberg, Schlenk, Stephenson, Woods, Northrup, Kunitz, Anson, Theorell, Lynen, Franke, Trolle and Harvey. Volume 6 gives detailed explanations of the preparation, purification, and properties of the many carbohydrases, nucleases, amidases, and proteases. Thrombase and the synthesizing enzyme oxynitrilase are also described. In Volume 7 are discussions (general and specific) of fermentation, glycolysis, anaerobic bacteria, dehydrases, cytochrome, and the isolatable oxyhydrases. A general review of the respiratory process is also given.



CHEMISTRY OF FOOD AND NUTRITION.
Sixth Edition.

By Henry C. Sherman. The Macmillan Company, New York. \$3.25. 8½ x 5½; x + 611; 1941.

By this latest revision, the sixth, the author has again brought up to date his well-known work. The four years which have elapsed since the appearance of the preceding edition (Q.R.B., Vol. 12, p. 383) have seen many new developments in the field of nutrition and the author has suc-

ceeded well in outlining and evaluating the recent discoveries. Almost every chapter has been revised and the latter half of the book has been rewritten to summarize the findings lately uncovered about vitamins, the B complex especially, and the so-called deficiency diseases. Included also is a new table on the copper and manganese contents of foods. The book is well documented and indexed and in all respects maintains a high standard as a college textbook.



LABORATORY DIRECTIONS FOR GENERAL ENDOCRINOLOGY.

By C. Donnell Turner. Student Book Exchange, Evanston, Illinois. \$1.50. 9 x 5½; v + 75; 1941 (paper).

Whether or not the author's arguments for the necessity of a course in general endocrinology for undergraduate students in zoology are generally held we cannot say, but it is upon this premise, and for this purpose that this manual has been prepared. The list of laboratory exercises has been designed to typify the procedures and techniques employed by present day research workers in the field of mammalian endocrinology. The rabbit, rat, and guinea pig are the primary subjects for experimentation, the work being divided into 44 exercises. This is to be supplemented by the study of histological sections of human material whenever available.



BIBLIOGRAPHY OF REFERENCES TO THE LITERATURE ON THE MINOR ELEMENTS AND THEIR RELATION TO PLANT AND ANIMAL NUTRITION. Second Supplement to the Third Edition.

Originally compiled by L. G. Willis. Chilean Nitrate Educational Bureau, New York. Free. 11 x 8½; 67; 1941 (paper).
This supplement (cf. Q.R.B., Vol. 15, p. 501 for mention of first supplement to third edition of this work) includes material that has accumulated since the first supplement was issued in 1940. The abstracts and references are obtained largely

from *Chemical Abstracts* and the *U. S. Experiment Station Record*, the source always being listed with each abstract. The index has been prepared with great care and will be found extremely useful to those working in this field. Following the plan originated in the first supplement a separate botanical index is included.



PROBLEMS AND TRENDS IN VIRUS RESEARCH.
University of Pennsylvania Bicentennial Conference, M-2.

By Thomas M. Rivers, Wendell M. Stanley, Wilbur A. Sawyer, Thomas Francis, Jr., Richard E. Shope, Joseph Stokes, Jr., and Geoffrey Rake. *University of Pennsylvania Press, Philadelphia.* 75 cents. 9 x 6; 75; 1941 (paper).

CHEMOTHERAPY. *University of Pennsylvania Bicentennial Conference, M-16.*

By E. K. Marshall, Jr., John S. Lockwood, and René J. Dubos. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 42; 1941 (paper).



SEX

SEX VARIANTS. A Study of Homosexual Patterns. In Two Volumes.

By George W. Henry. *With Sections Contributed by Specialists in Particular Fields. Sponsored by Committee for the Study of Sex Variants, Inc., Paul B. Hoeber (Medical Book Department of Harper and Brothers), New York and London.* \$12.50 for the two volumes. 9½ x 6; Vol. I: xxii + 546; Vol. II: viii + 633; 1941.

In the "Impressions" at the close of Volume II it is indicated that law and society have failed to solve the problems connected with homosexuality. In these two volumes a start toward a scientific approach to a solution has been attempted. Complete case studies of 80 homosexual persons are presented. Volume I contains the histories of 40 males and Volume II of 40 females; in each case the individuals are grouped according to whether they were bisexual, homosexual, or narcissist. For each individual a genetic chart, records of general im-

pressions, the family background, personal history, physical examination (including a special study of the sex characteristics) and roentgenological study, and a summary are included. At the end of the second volume there are a number of collected studies, a brief chapter on "impressions" gained from the cases presented, and several appendices. The latter include discussions of masculinity-femininity tests, physical characteristics suggesting masculinity or femininity (with photographs), and anthropological data; a chapter on internal pelvic measurements of sex variants, by G. W. Henry, R. P. Ball, and J. R. Carty; a chapter on the gynecology of homosexuality, by Robert L. Dickinson; and a glossary of "the language of homosexuality" and a slang vocabulary.

In the "Impressions" the author expresses his view that the sex variant seems to be a by-product of civilization.

In our present civilization he is an expression of his inability to meet the responsibility of establishing and maintaining a home which involves the rearing of children. The manifold demands made upon parents as a result of our high standards of living often discourage heterosexual adjustment and foster substitute sexual activity.

Query: Are there no homosexuals among primitive peoples?

Another interesting observation is:

All persons who manifest violent emotional reactions to the sex variant warrant serious consideration. Such persons may be reacting to personal experience or they may be on the defensive lest they disclose their own unconventional desires and impulses.

These volumes are obviously and primarily for members of the medical profession and social welfare workers. The preparation of a third volume to discuss the results of these investigations is anticipated.



SPERMATOOA AND STERILITY. A Clinical Manual.

By Abner I. Weisman. *With a Foreword by Robert L. Dickinson. Paul B. Hoeber (Medical Book Department of Harper and Brothers), New York and London.* \$5.50. 9½ x 5½; xvi + 314; 1941.

Leeuwenhoek first saw human spermatozoa almost 300 years ago, their function in reproduction has been definitely established for a long time, and yet it is only in recent years that any interest in the sperm cells and their contribution to sterility has been aroused. The meagerness of the available information becomes evident when one examines this book in which the author brings together and critically reviews the facts and ideas so far acquired about the subject.

The primary purpose is to give to the general clinician as well as to the specialist in urology and gynecology a broad view of the anatomy, physiology and biochemistry of sperm cells with reference to the processes of fertilization. Most of the book is devoted to the description of techniques for the collection and analysis of semen and the methods of diagnosing sterility in the male. Therapy in cases of sterility is also discussed and, in addition, there are chapters on the spermicidal action of certain drugs, on the study of semen in legal medicine, and on pregnancy tests. This work represents a pioneer enterprise and therefore is expected to be faulty in some respects. Nevertheless it serves to stabilize the scattered ideas on the subject and to lay the foundation for more adequate investigations. An excellent list of references is included.



FEMALE SEX HORMONES. *University of Pennsylvania Bicentennial Conference, M-6-7.*

By Edward A. Doisy, Philip E. Smith, Robert T. Frank, and Elmer L. Sevringhaus. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 58; 1941 (paper).



BIOMETRY

THE BULLETIN OF MATHEMATICAL BIOPHYSICS. *Volume 3, Number 4, December, 1941.*

Edited by N. Rashevsky. *University of Chicago Press, Chicago.*

This number contains the following pa-

pers: A Neural Mechanism for Discrimination: IV. Monocular Depth Perception, by Henry Stanton; Some Preliminary Considerations Concerning Concentration of Oxygen in Tissue, by Ingram Bloch; Note on a Possible Application of Some Concepts of Topology to Asymmetric Organization of Protoplasm, by G. F. Gause; Statistical Distribution of Impedance Elements in Biological Systems, by A. M. Weinberg and A. S. Householder; A Theory of Steady-State Activity in Nerve-Fiber Networks: III. The Simple Circuit in Complete Activity, by Alston S. Householder; Distribution of Response Times, by H. D. Landahl; Application of the General Fluid Circuit Theory to the Chloride-Bromide-Deuterium Oxide Experiment, by H. C. Peters; The General Membrane Equilibrium Equation: Its Simple Derivation and Some of Its Biological Implications, by M. F. Morales and N. W. Shock.



STATISTICAL CALCULATION FOR BEGINNERS.

By E. G. Chambers. *The University Press, Cambridge; The Macmillan Co., New York.* \$2.00. 8½ x 5½; vii + 110; 1940.

The purpose of this book, "to explain as simply as possible how to perform the calculations involved in the commoner statistical methods," is amply fulfilled by the writer. No attempt is made to give the mathematical basis of the techniques used. The subjects covered in the 92 pages are: averages, scatter, normal distribution, significance of mean and mean difference, correlation, regression and correlation ratio, chi square, contingency, and goodness of fit. The problems after each section (the answers being found at the end of the book) add to its teaching value. Four appendices of tables and one of numerical material for exercises are present. The volume is indexed.



PSYCHOLOGY AND BEHAVIOR

THE MASK OF SANITY. *An Attempt to Reinterpret the So-called Psychopathic Personality.*

By *Hervey Cleckley*. C. V. Mosby Co., St. Louis. \$3.00. 8½ x 5½; 298; 1941.

In this book the problem presented by the type of individual on whom the psychiatrist makes the diagnosis "psychopathic personality" is considered. From the legal point of view these individuals are classed as sane, competent, and responsible for their own conduct. Examination of their life-stories reveals the fact that, even in the face of good intelligence, excellent opportunities, well-wishing friends and relatives who outdo themselves to help them to their feet, and the absence of any recognized psychosis or psychoneurosis, these individuals repeatedly fail to manage themselves and their responsibilities in a competent and satisfactory way. Since they are legally sane they are not eligible for admission to many state and federal hospitals, cannot be held for treatment when they are admitted, and are constantly being thrown back on the care of their families and communities.

Cleckley presents nine brief case abstracts of individuals who are so completely psychopathic in their behavior that they are unable to manage themselves, except for brief intervals, over many years, and whose records show repeated incarcerations and hospitalizations. In addition six cases are described of individuals who are able to keep up a front and carry their responsibilities in their communities, but who, in their private lives, show the typical irresponsible psychopathic behavior, usually associated with the use of alcohol. In Chapter 22 the typical and outstanding features of the patients under discussion are summarized. In the final chapters of the book Cleckley discusses possible psychodynamic factors. He suggests the term "semantic dementia" for this group of patients that, basically, seems devoid of all capacity to experience values and meaning in life, and recommends that they be considered, medically, as belonging to the psychotic group.

This book represents an incisive attempt to clarify a difficult problem with which so much confusion is associated, and should stimulate further thought and action on the part of psychiatrists generally. References to the literature are presented in footnotes and there is an index.

CONDITIONED REFLEXES AND PSYCHIATRY. *Lectures on Conditioned Reflexes, Volume II.* By *Ivan P. Pavlov*. Translated and Edited by *W. Horsley Gantt*. International Publishers, New York. \$4.00. 9½ x 6; 199; 1941.

When the history of the science of this epoch is written Pavlov will, without doubt, be ranked among the greatest of the biologists. His intellectual eminence was recognized long before his death and is even better appreciated in this book which contains selected addresses and unpublished papers prepared between 1928 and his death in 1936. Having carefully and thoroughly explored the mechanism of the reflexes, toward the end of his life Pavlov sought to apply the knowledge gained to the problems of human behavior and psycho-pathology. The papers which Gantt has assembled refer to this aspect of Pavlov's work. The articles are especially concerned with the relationship between the reflex mechanism and the functions of the nervous system and cortical centers. Pavlov's well-known experiments on the production of neurosis and his attempts to interpret, on the basis of these experiments, the manifestations of neurosis in man are summarized. There is no formal connection between the series of papers included in the volume, and so it is impossible in the space of a brief review to outline satisfactorily the contents. It can be said, however, that each of the articles reveals Pavlov's intentions to demonstrate the validity of investigating psychiatric and, in general, behavioristic problems by the experimental approach. Gantt, who has translated the articles and edited the volume, contributes an introduction in which he reviews Pavlov's work and clearly brings out its significance. This volume, together with the preceding one published in 1928, embodies all of Pavlov's public lectures from 1903 to 1936.



ANIMAL BEHAVIOUR. *Impulse. Intelligence. Instinct.*

By *Johann A. Looser*. The Macmillan Co., New York and London. \$2.00. 8½ x 5½; x + 178; 1940.

In this posthumous publication one finds an adequate summary of Loeser's ideas on animal behavior and of the kinds of facts on which his conclusions are based. The explanation of why animals act as they do has reflected the philosophy and also the theology of the period of the observer. Confronted, for example, by the seasonal migration of birds or their nest building, observers have introduced the concept of instinct, tropism, reflex, etc. In Loeser's views one almost sees the reverberations of the uncertainty principle. In agreement with some modern students of the subject he assumes that the reaction of an animal is to be regarded as the manifestation of a purposive act inasmuch as it is the resultant of a number of small voluntary acts. "These 'small actions', combined with a specific physical constitution which becomes effective in the animal's natural surroundings unite to produce one biologically purposive action." The author attempts to demonstrate the validity of this view by examining overt activities associated with self-preservation, reproduction, sociality, and migration. Some students of the subject accept this theory while others do not. As stated, it does not add much to a clarification of the question. When it is postulated that the overt activity of the animal is also a function of the physical constitution some will conclude that the concept of instinct thrown out of the door has reentered by the window.



FACTORIAL STUDIES OF INTELLIGENCE. *Psychometric Monographs, Number 2.*

By L. L. Thurstone and Thelma G. Thurstone. *University of Chicago Press, Chicago.* \$1.50. 9½ x 6½; v + 94; 1941 (paper).

No single index designed to measure mental ability can give a true picture of an individual's mental endowment. Such an index might stamp the individual as below average, whereas he may be far above average in some specific aptitude. Tests which will pick out such specific factors in mental ability are of special significance in numerous fields, important among which is vocational guidance.

The authors of this monograph have for several years been engaged in such factorial studies of intelligence, and they have with considerable success isolated a number of primary abilities among college students. The present investigation was designed to determine whether these primary abilities could be identified in elementary school subjects, and whether some of the original conclusions could be sustained. The 60 tests which were devised are described briefly. Seven primary factors in mental ability were studied, and it was found that three of the tests could be selected for each ability, having a high saturation for one particular ability and a low saturation for the remaining six. Thus the writers have shown that, with a battery of 21 tests, several of the many factors in intelligence can be picked out with some degree of success on school children. This investigation indicates broad possibilities for the use of factor analysis in related fields.



COMPANIONSHIP PREFERENCE AND DOMINANCE IN THE SOCIAL INTERACTION OF YOUNG CHIMPANZEES. *Comparative Psychology Monographs, Volume 17, Number 1. Serial Number 85.*

By Vincent Noulis. *Williams & Wilkins Company, Baltimore.* 10 x 6½; 57; 1941 (paper).

For this study in social behavior, five pre-adolescent chimpanzees (two males, two females, and one male castrate) were used. Data were collected with regard to companionship preferences, dominance status, food sharing, and general behavior. The method of paired companions was successfully used in the investigation, and second-by-second records of the behavior of the animals were made. Significance tests are applied to the statistical data whenever possible, and the results are presented in the light of such analysis.

Among conclusions worthy of note are the following: (1) each animal exhibited a consistent preference for one other animal, although this preference was seldom mutual; (2) the five animals were ranked in a consistent, progressive order of dominance by two separate tests of dominance

status, and no relationship was found between preference status and dominance; (3) food sharing was exhibited only by subordinate animals to their dominate partners, and no relationship was found to exist between preference status and food sharing; and (4) with regard to general social behavior, the larger portion of time was spent in grooming and play-fighting.

A bibliography of 36 titles is appended.



FACTOR ANALYSIS TO 1940. *Psychometric Monograph No. 3.*

By Dael Wolfe. University of Chicago Press, Chicago. \$1.25. $9\frac{3}{4} \times 6\frac{3}{4}$; vii + 69; 1940 (paper).

It is universally accepted that ability in any field is determined by some combination of aptitudes or faculties. These several factors may be separated to some degree by specific tests. A statistical analysis may then be made of the efficacy with which these tests isolate the factors. This monograph is a review of the literature on factor analysis and discusses the following questions:

1. What is the reasoning common to the different factor methods?
2. How do the several methods differ from one another?
3. How may factors best be interpreted?
4. What have been the chief results of factor analysis?
5. What are the limitations and uses of factor analysis?

The author omits the detailed statistical procedures employed by workers in this field, and treats the subject as non-technically as possible. He clearly describes the advantages and disadvantages of each method of treatment.

So far factor analysis has had but limited practical application, this mainly in psychological research. The principal users of the method feel, however, that its future significance is as an exploratory instrument in the field of scientific research. It may point out certain underlying factors and relationships which may then be studied in the laboratory. The paper contains a complete index and a bibliography of 530 titles.

WOLF CHILD AND HUMAN CHILD. *Being the Narrative Interpretation of the Life History of Kamala, the Wolf Girl.*

By Arnold Gesell. Harper and Brothers, New York and London. \$2.00. $10 \times 6\frac{7}{8}$; xvi + 107; 1941.

An account is presented, in narrative form, based on the diary kept by the missionary who found and cared for them in his orphanage in India, of the development until their death of two human children who were living in a den of wolves. One child, Amala, died the first year at the age of two, but the other, Kamala, who was eight when she was found, lived to the age of seventeen. It is her story, chiefly, that Gesell has reconstructed from the missionary's notes into a psychological biography. The gradual weaning of this child from the feral characteristics she showed when she first came to the orphanage to the ways of a human child make a fascinating and provocative story. Gesell follows out some of the broader connotations of this story in a chapter in which the interrelationship of heredity and culture are discussed. He states: "From the standpoint of genetic and clinical psychology the most significant phenomenon in the life career of Kamala is the slow but orderly and sequential recovery of obstructed mental growth." References to the other cases of feral and isolated children are made but there is no bibliography and source material is only occasionally quoted directly. The book is illustrated.



THE FACTORS OF THE MIND. *An Introduction to Factor-Analysis in Psychology.*

By Cyril Burt. The Macmillan Co., New York. \$5.00. $8\frac{1}{2} \times 5\frac{1}{2}$; xiv + 509; 1941.

Factor-analysis as a psychological methodology is presented in this book not merely as a statistical technique but as a mode of logical reasoning appropriate to the field of psychology. The material is organized in three parts: (I) The logical and metaphysical status of factors in psychology, (II) The relations between different methods of factor-analysis, and (III) The distribution of temperamental types. The

author states: "My primary object has been to determine a little more exactly the nature of so-called mental 'factors' by examining the form of proof by which those 'factors' are established." He carefully delimits the utility of factor-analysis, stressing its value for more precise and systematized description of the general structure of the mind or of the population, and minimizing its inferential and predictive use. There are two appendices: Appendix I. Working methods for computers, and Appendix II. Analysis of a matrix into its latent roots and latent vectors. The list of references includes 139 titles and there are author and subject indices.

A lucid and informative presentation of current viewpoints in this interesting field of psychological research.



INDIVIDUAL DIFFERENCES IN EMOTIONALITY, HYPOTHESIS FORMATION, VICARIOUS TRIAL AND ERROR, AND VISUAL DISCRIMINATION LEARNING IN RATS. *Comparative Psychology Monographs, Volume 17, Number 3, Serial Number 87.*

By Frederic M. Geier, Max Levin, and Edward C. Tolman. Williams & Wilkins Company, Baltimore. 50 cents. 10 x 6½; 20; 1941 (paper).

Using 57 male albino rats, these investigators were able to make 29 different measures of emotionality, vicarious trial and error, hypothesis formation, and discrimination learning. The data are presented in the light of tetrachoric correlations and "cluster-orthometric" analyses. A new form of graphic presentation, the factorgram, has been used to show graphically the extent of structural similarities of the variables. Among the significant conclusions of the report, the following appear most important: (1) timidity contributes neither negatively nor positively to learning or vicarious trial and error; (2) strong motivation (food) is a partial determiner of cognitive reaction; and (3) learning capacity in rats seems always to be relatively specific to the problem.

A short list of references concludes the monograph.

CRIMINAL YOUTH AND THE BORSTAL SYSTEM.

By William Healy and Benedict S. Alper. *The Commonwealth Fund, New York; Oxford University Press, London.* \$1.50. 8½ x 5½; 251; 1941.

This book represents the results of a study made for the Criminal Justice-Youth Committee of the American Law Institute of the English Borstal System for training criminal youth. The purpose of the book is to consider possibilities for more effective methods of dealing with criminal youth in this country. The book is organized into three parts. In Part I, The Challenge, the present-day problem and ways it is being met in the United States are presented. In Part II, The Borstal System, the English handling of the same problem is described in detail. The origin and growth of the Borstal idea is presented, the general principles of Borstal training are outlined and the relationship of the boys to the staff, their homes and communities discussed. In Part III, Effective Training and Treatment, the Borstal system is critically evaluated and the desirability of incorporating its basic features into our own training institutions stressed. There is a bibliography and an index.



HUMAN NATURE IN THE LIGHT OF PSYCHOPATHOLOGY.

By Kurt Goldstein. *Harvard University Press, Cambridge.* \$2.50. 7½ x 5; x + 258; 1940.

In this book, which comprises the William James Lectures delivered at Harvard University in 1938-1939, the author presents his conception of the nature of man which has evolved out of years of experience in the field of psychopathology and organic brain disease. He is concerned both with the proper methodology of research in studying human nature and with the ultimate views he has reached. His approach is essentially holistic. The basic generalization which he reaches is that abstract behavior represents the highest capacity of the human being. Of particular interest are his discussions of anxiety and fear, and of adaptation to the world. The chapters

on motivation and on the structure of the personality seem to contribute the least. The two final chapters, The individual and others and The fallacy of "Isolation" in social philosophy, are more philosophical in their orientation. Notes for each chapter are included and there is an index.



FORM DISCRIMINATION AS A LEARNING CUE IN INFANTS. *Comparative Psychology Monographs, Volume 17, Number 2, Serial Number 86.*

By Bing-Chung Ling. *The Williams & Wilkins Co., Baltimore.* \$1.50. 10 x 6 $\frac{1}{2}$; 66; 1941 (paper).

This monograph reports a study of geometric form discrimination in infants. Over fifty infants, ranging in age from six to twelve months, participated in the study which lasted fourteen months. Six series of experiments were used involving changes in the experimental blocks in respect of spatial arrangement, size, number, and order. The data obtained were analyzed in detail and the conclusions presented under two headings: A. Perceptual processes, and B. Learning processes. Of particular interest is the evidence pointing to a capacity for abstraction in the infants within the age levels studied. This study represents an interesting contribution to the problem of the thinking function in the first two years of life. There is a bibliography of 65 titles.



LIONS ON TRUST.

By Cleland Scott. *The Macmillan Co., New York.* \$3.00. 8 $\frac{1}{2}$ x 5 $\frac{1}{2}$; 317; 1940. A great deal of interesting, detailed information regarding the behavior of wild and of domestic lions. The author has hunted lions on and near his large farm in East Africa and has raised them to adulthood as "pets" in his home. He stresses the conclusion that lions can differ individually to a remarkable extent. The book contains also a good chapter on game preservation and many unusual remarks on the behavior of hunters.

THERAPEUTIC ADVANCES IN PSYCHIATRY. *University of Pennsylvania Bicentennial Conference, M-3.*

By Edward A. Strecker, Abraham A. Brill, Nolan D. C. Lewis, and Arthur H. Ruggles. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 34; 1941 (paper).

THE BEGINNINGS OF SOCIAL BEHAVIOR IN UNICELLULAR ORGANISMS. *University of Pennsylvania Bicentennial Conference N-C.*

By Herbert S. Jennings. *University of Pennsylvania Press, Philadelphia.* 25 cents. 9 x 6; 17; 1941 (paper).



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A HISTORY OF MAGIC AND EXPERIMENTAL SCIENCE. *Volumes V and VI. The Sixteenth Century.*

By Lynn Thorndike. *Columbia University Press, New York.* \$10.00 for the two volumes. 8 $\frac{1}{2}$ x 5 $\frac{3}{8}$; Vol. V: xxii + 695, Vol. VI: xviii + 766; 1941.

Volumes III and IV of this work dealing with the 14th and 15th centuries have already been reviewed in these columns (cf. Q. R. B., Vol. 10, p. 375). Further notice seems called for, however, owing to the fact that the sixteenth century, the subject of the last two volumes, marks a critical period in the development not only of scientific thought but of belief in magic as well.

The attitude of the modern devotee of magic is not so much unscientific as frankly anti-scientific. This is due somewhat to the tendency of modern science to become esoteric, owing to the placement of emphasis on the acquisition of knowledge to the neglect of its dissemination. There is a certain type of mind that seems actuated by a sort of professional jealousy, which realizes unwillingly its intellectual inability to keep abreast of advancing scientific thought, and which, therefore, resorts to a belief in magic as a means of compensation. A belief in the supernatural is a logical corollary.

In the mediæval period belief in magic did not necessarily imply belief in the supernatural. The authenticity of magi-

cal phenomena was accepted, but these were interpreted as the result of natural factors as yet unknown. Today, belief in magic is incompatible with belief in science, but in the dark ages the magician and the scientist were generally blended in the same individual. Goethe's great dramatic poem celebrates a philosopher whose activity was devoted equally to the search for the elixir of life and the extermination of malaria.

The story is frequently told of how Kepler, the greatest astronomer of his time, had to choose between casting horoscopes for the European nobility or death by starvation, and there has been much speculation as to how distasteful such work must have been to one of his mentality. But the truth is that Kepler probably shared the faith of his most superstitious patrons in his occult prognostications. The difference between Kepler and the modern fortune-teller is that Kepler believed that the planets were in some mysterious but natural way connected with human welfare, and that by formulating his laws of planetary motion he might be able to throw light on this connection, whereas the astrologer believes the connection to be supernatural, and therefore not amenable to scientific investigation.

The alliance between science and magic was of course only a temporary one. That it lasted as long as it did was owing to the reliance of both on authoritarianism. As long as Aristotle, Hippocrates, Pliny, and Galen constituted the supreme court of last resort in the settlement of disagreements about scientific matters, the wheat and the tares could continue to grow together in amity, but when Galileo dropped his balls from the tower of Pisa it became inevitable that science and magic should arrive at the parting of the ways. The history of the sixteenth century is the story of the divarication between two incompatible types of human mind. Now what were some of the beliefs that the sixteenth century savants accepted? Thorndike enumerates many of them. They were chiefly of a biological nature—that salamanders can live in fire; that corpses will bleed in the presence of a murderer; that mice, flies, and worms can be spontaneously generated

from putrefaction, and birds from driftwood; that geese come from barnacles, etc. There was also a considerable body of quack medicine that seems like an adumbration of "The Long Lost Friend"—which of course it was—such that peony and emerald, the lungs of a fox, and the dung of a white dog are specific medicine for epilepsy, asthma, and quinsy, respectively; that wearing a belt made of wolf's intestine will cure colic; and that hydrophobia can be contracted by sleeping beneath a tree whose bark has been chewed by a rabid dog. From the standpoint of folk-lore perhaps the most interesting item is that if a female snake, during copulation, bites off and swallows the head of the male, the first act of the progeny will be to avenge the death of their sire by killing the dam—a strange transference of the Orestes myth to zoology. The thoroughness with which Thorndike has covered this field is testified to by the index to all six volumes which appears at the end of the last. It occupies 149 pages, and as about 40 authors per page appear among the entries, it serves as a bibliography of nearly 6000 items. It is difficult to imagine a scholar in any field at all who could not find something of interest to his work in this monumental book.



ANTITHETICAL VIEWS ON TWINNING FOUND IN THE BIBLE AND SHAKESPEARE. Reprinted from *Southern Medicine and Surgery*, Volume 103, Number 3, 1941.

By Groesbeck Walsh and Robert M. Pool. Obtainable from the Authors, Fairfield, Alabama. Free. 10½ x 7½; 10; 1941 (paper).

That Shakespeare was a student of the Scriptures and extensively influenced by them is a well-authenticated fact. In at least one respect, however, he did not show the traditional views of the Old Testament Hebrews. This is indicated by his treatment of the personalities of the three pairs of twins that figure in two of his comedies. There are no twins in his tragedies. On the other hand, the only two pairs of twins in the Scriptures are tragic figures.

The strong ties of family love that unite Sebastian and Viola contrast widely with the jealousy of Jacob toward Esau, a jealousy which survives today between the Zionists and the Arabs in Palestine. The story of Jacob and Esau is generally considered to be epic history of the beginning of the strife between Israel and Edom, but the present writer believes that the somewhat similar story of Phares and Zerah who did not become the progenitors of a family feud indicates that the question goes much deeper, and its answer involves a study of the folk-lore of both peoples, as well as of such matters as mancinism and freemartinry, and various references to twins, not only in the two authors concerned, but also in the works of Mahomet and H. H. Newman.

Despite the thoroughness of the authors in this piece of research, the reader is left with the feeling that there is still more to be said in this matter. Why, for instance, is it considered disadvantageous for a javelin thrower to be lefthanded, and at the same time an advantage to the slinger? And what is the evidence that Simon Peter was left-handed? And why did Ehud, who was left-handed, carry his dagger on his right thigh? Let us hope that these matters have been elucidated in the additional manuscript which the authors have prepared and for which they are seeking a publisher.



THE DEVELOPMENT OF THE SCIENCES. *Second Series.*

Edited by L. L. Woodruff. Yale University Press, New Haven. \$3.00. 9 x 5½; 336; 1941.

This is a splendid piece of work that cannot be too enthusiastically recommended. Within the past few years a great many books have been reviewed in these columns, all of which have had the same end in view—to give a more or less detailed general survey of the universe as contemplated by modern science. But modern science is a very complex thing, especially as the result of new discoveries and theories based upon them in the last few years, and many of the older generation have dif-

ficulty in recasting their ideas so that they may read these modern works intelligently.

The work now under discussion approaches the problem from the historical standpoint. It puts the main emphasis not on what the teaching of modern science is, but how it came about. Its outlook is dynamic rather than static, and readers who wish to acquire a familiarity with present day science are urgently advised to begin by reading this symposium. Its eight chapters deal with mathematics, astronomy, physics, chemistry, geology, biology, psychology, and medicine. The important incidents in the careers of those who founded and developed these sciences are recounted. The wealth of biographic material brings these characters to life again in the reader's imagination. The book is well documented and provided with index and bibliography.



RUBBER AND ITS USE.

By Harry L. Fisher. Chemical Publishing Company, Brooklyn, N. Y. \$2.25. 8½ x 5½; xvi + 128; 1941.

This is a book that grew out of the experiences of the author during his seventeen years as a research chemist in lecturing on the chemistry and technology of rubber. He discusses in order: the history of the rubber industry, sources and production of crude rubber, properties of crude and vulcanized rubber, the importance of vulcanization, compounding and vulcanizing rubber, manufacturing rubber, latex manufacturing processes, synthetic rubbers, and various rubber derivatives. This volume should prove most interesting and useful not only because of its authoritative and practical treatment but because its style is such that it can be read and easily understood by the general reader. The new developments in synthetic rubber which are here described should prove of especial interest and value to laymen in view of the constant and ever-increasing emphasis on this important phase of the rubber industry. The book is appropriately illustrated and there is a very helpful list of reference works for supplementary reading. A very complete index concludes this timely work.

DER GESTALTKEIS. *Theoria der Einbeit von Wahrnehmen und Bewegen.*

By Viktor von Weizsäcker. Georg Thieme Verlag, Leipzig. RM 9.00 (cloth); RM. 7.50 (paper) (outside of Germany). 9 $\frac{1}{2}$ x 6 $\frac{1}{2}$; viii + 179; 1940.

The author develops his philosophy on the "Gestalt Cycle" from a study of pathological conditions of the nervous system, and conditions for perception and for motion (anatomical, physiological, and in terms of space, time, and form). Perception and motion are explained as manifestations of a resting state. Like Parmenides, he understands by "existence" universal, immutable, invariable being, and the progressive changes we perceive in "life" (between birth and death) as a semblance of existence.



DIE BIBLIOTHEK EINES WITTENBERGER MEDIZINERS UM 1790 (*Chr. Fr. Nürnberger*). *Abhandlungen zur Geschichte der Medizin und der Naturwissenschaften*, Heft 33.

By Heinrich Kramm. Verlag Dr. Emil Ebering, Berlin. RM. 3.90. 9 $\frac{3}{8}$ x 6 $\frac{1}{4}$; 96; 1940 (paper).

This list of 471 individual books and sets on scientific subjects, presented by Christian F. Nürnberger (1744-1795) to the library of Wittenberg University, Halle, is preceded by an introductory chapter on the history of the University Library, mention of collections presented by other persons, and a brief sketch of the life of the donor of this collection. It is of interest mainly to the medical historian.

STUDIES IN THE HISTORY OF SCIENCE. *University of Pennsylvania Bicentennial Conference.*

By E. A. Speiser, Otto E. Neugebauer, Hermann Ranke, Henry E. Sigerist, Richard H. Stryck, Everts A. Graham, Edgar A. Singer, and Hermann Weyl. *University of Pennsylvania Press, Philadelphia.* \$1.50. 9 x 5 $\frac{1}{2}$; 123; 1941.

This is a series of lectures on different phases of the history of science. They are not connected except that they were all given at the bicentenary of the University of Pennsylvania. They are well documented but there is no index or bibliography.



ADVENTURES IN GOOD EATING. *Good Eating Places along the Highways of America.* Eighth Edition.

By Duncan Hines. *Adventures in Good Eating, Inc., Bowling Green, Kentucky.* \$1.50. 7 $\frac{1}{2}$ x 5; 316; 1941 (paper).

LODGING FOR A NIGHT. *A Directory of Hotels Possessing Modern Comforts, Inviting Cottages and Modern Auto Courts, also Guest Houses Whose Accommodations Permit the Reception of Discriminating Guests.* Fourth Edition.

By Duncan Hines. *Adventures in Good Eating, Inc., Bowling Green, Kentucky.* \$1.50. 7 $\frac{1}{2}$ x 5; 318; 1941 (paper).

A CHALLENGE TO SCHOLARSHIP. *University of Pennsylvania Bicentennial Conference, M-D.*

By W. Mansfield Clark. *University of Pennsylvania Press, Philadelphia.* 50 cents. 9 x 6; 20; 1941 (paper).



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